The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

Editor
John D. Mizelle, Zoology

ASSOCIATE EDITORS

Edward Albert Chapin, Washington, D. C. ..... Entomology
Albert L. Delisle, Notre Dame, Ind. ..... Plant Morphology
Carroll Lane Fenton, New Brunswick, N. J. ... Invertebrate Paleontology
John Hobart Hoskins, Cincinnati, Ohio ..... Paleobotany
George Neville Jones, Urbana, Ill. ..... Plant Taxonomy
Remington Kellogg, Washington, D. C. ..... Mammalogy
Jean Myron Linsdale, Robles del Rio, Calif. ..... Ornithology
George Willard Martin, Iowa City, Iowa ..... Mycology
Hugh M. Raup, Petersham, Mass. ..... Plant Ecology
Karl Patterson Schmidt, Chicago, Ill. ..... Ichthyology and Herpetology
Harley Jones Van Cleave, Urbana, Ill. ..... Invertebrate Zoology

Vol. 45, 1951

(January - May)

PUBLISHED BY THE UNIVERSITY OF NOTRE DAME
NOTRE DAME, INDIANA

CONTENTS

No. 1, January, 1951

Notes on Nearctic Hepaticae III. A Conspectus of the Family Lophoziaceae, With a Revision of the Genera and Subgenera ..... Rudolf M. Schuster 1

Ficus in Florida—III. Asiatic Species ..... Mary F. Barrett 118

On the Cytotaxonomy of the genus Corydalis, Section Eucorydalis ..... Gerald B. Ownbey 184

An Ecological Survey of the Fort Leavenworth Military Reservation ..... Malcolm J. Brumwell 187

The Biology of Leiolopisma laterale (Say) ..... Thomas Howard Lewis 232

Amphibians and Reptiles of a Fifteen-Acre Tract in Georgia .... Wilfred T. Neill 241

Notes on a Collection of Reptiles and Amphibians from Princess Anne County, Virginia ..... John E. Werler and James McCallion 245

Hymenolepis hopkinsi, n. sp., a Cestode from the Black Duck ..... Everett L. Schiller 253

No. 2, March, 1951

A Revision of the Nearctic Oedemeridae (Coleoptera) ..... Ross H. Arnett, Jr. 257

Nevada Dytiscidae (Coleoptera) ..... Ira La Rivers 392

A Revision of the Nearctic Species of the Genus Gaurax (Diptera, Chloropidae) ..... Curtis W. Sabrosky 407

Note on the Method of Colony Foundation of the Ponerine Ant Amblyopone australis Erichson ..... Caryl P. Haskins and Edna F. Haskins 432

The American Cyprinid Fish Notropis germanus Hay, Interpreted as an Intergeneric Hybrid ..... Carl L. Hubbs 446

The Range of Cryptobranchus bishopi and Remarks on the Distribution of the Genus Cryptobranchus ..... I. Lester Firschein 455

Observations on a Captive Gila Monster ..... Floyd E. Durham 460

An Abnormal Earthworm ..... G. E. Gates 471

The Cespitose Lupines of Western North America ..... LeRoy E. Detling 474

Additional Records of Some Illinois Vascular Plants ..... G. N. Jones, H. E. Ahles, G. D. Fuller and G. S. Winterringer 500

New and Infrequently Collected Illinois Plants ..... Glen S. Winterringer 504

Notes and Discussion

Addendum to "The Loci of Contact Chemoreceptors in Insects" ..... Hubert Frings and Mable Frings 507

Records of Aristida oligantha Michx. in St. Joseph County, Indiana ..... A. L. Delisle 508

The Ornate Box Turtle, Terrapene ornata (Agassiz) in Indiana ..... James C. List 508

Book Reviews 509

No. 3, May, 1951

Locomotion and Appendicular Anatomy in Three Soricoid Insectivores ..... Charles A. Reed 513

Observations on the Breeding Habits of the Red-eyed Towhee ..... Roger W. Barbour 672

A Systematic Study of the Main Arteries in the Region of the Heart—Aves XXII. Passeriformes—Corvidae, Part I ..... Fred H. Glenny 679

Distribution of the Carabidae (Coleoptera) of Boulder County, Colorado ..... Verna Lee Haubold 683

Studies on Metacercariae of Perca flavescens in Lake Itasca, Minnesota ..... Asa C. Chandler 711

Geographical Affinities of the Flora of North Dakota ..... Velva E. Rudd 722

New Combinations in Salix (Sections Pellitae and Phylicifoliae) ..... Carleton R. Ball 740

A Natural Hybrid of Liatris (x L. Weaveri Shinners) ..... L. O. Gaiser 750

Book Reviews 764

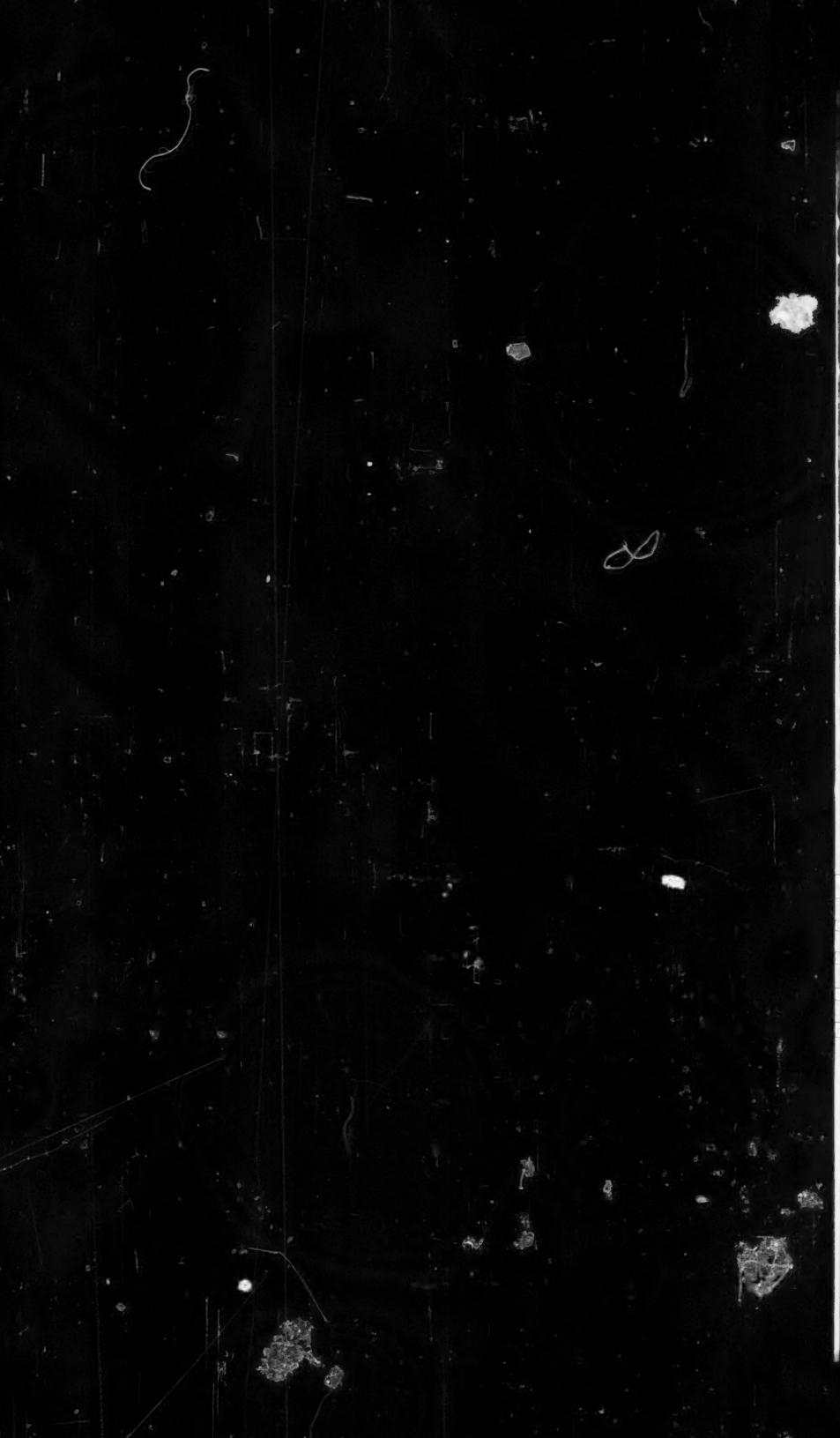
Dates of Publication

Volume 45, 1951

January ..... February 21

March ..... June 6

May ..... July 26



UNIVERSITY
OF MICHIGAN

MAR 1951

SCIENCE
LIBRARY

The
American Midland Naturalist

Founded by J. A. Nieuwland, C. S. C.

John D. Mizelle, *Editor*

CONTENTS

Notes on Nearctic Hepaticae III. A Conspectus of the Family Lophoziaceae, With a Revision of the Genera and Subgenera ..... Rudolf M. Schuster 1

Ficus in Florida—III. Asiatic Species ..... Mary F. Barrett 118

On the Cytotaxonomy of the genus Corydalis, Section Eucorydalis ..... Gerald B. Ownbey 184

An Ecological Survey of the Fort Leavenworth Military Reservation ..... Malcolm J. Brumwell 187

The Biology of Leiolopisma laterale (Say) ..... Thomas Howard Lewis 232

Amphibians and Reptiles of a Fifteen-Acre Tract in Georgia ..... Wilfred T. Neill 241

Notes on a Collection of Reptiles and Amphibians from Princess Anne County, Virginia ..... John E. Werler and James McCallion 245

Hymenolepis hopkinsi, n. sp., a Cestode from the Black Duck ..... Everett L. Schiller 253

Vol. 45 January, 1951 No. 1

EDITORIAL STAFF

JOHN D. MIZELLE ..... *Zoology*
Editor, University of Notre Dame, Notre Dame, Ind.

EDWARD A. CHAPIN ..... *Entomology*
U. S. National Museum, Washington, D. C.

ALBERT L. DELISLE ..... *Plant Morphology*
University of Notre Dame, Notre Dame, Ind.

CARROLL LANE FENTON ..... *Invertebrate Paleontology*
404 Livingston Ave., New Brunswick, N. J.

JOHN HOBART HOSKINS ..... *Paleobotany*
University of Cincinnati, Cincinnati, Ohio

GEORGE NEVILLE JONES ..... *Plant Taxonomy*
University of Illinois, Urbana, Ill.

REMINGTON KELLOGG ..... *Mammalogy*
U. S. National Museum, Washington, D. C.

JEAN MYRON LINSDALE ..... *Ornithology*
Hastings Reservation, Monterey, Calif.

GEORGE WILLARD MARTIN ..... *Mycology*
State University of Iowa, Iowa City, Iowa

HUGH M. RAUP ..... *Plant Ecology*
Harvard Forest, Harvard University, Petersham, Mass.

KARL PATTERSON SCHMIDT ..... *Ichthyology and Herpetology*
Chicago Natural History Museum, Chicago, Ill.

HARLEY JONES VAN CLEAVE ..... *Invertebrate Zoology*
University of Illinois, Urbana, Ill.

NOTE: THE AMERICAN MIDLAND NATURALIST, published by the University of Notre Dame is primarily, though not exclusively, devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, three of which make up a volume.

Authors are invited to submit carefully prepared manuscripts and requested to limit tables and illustrations as much as possible. Abstracts and reprint orders should accompany manuscripts or corrected proofs.

The following numbers are out of print: Vol. 1 (1, 4, 5, 8-12); Vol. 2 (1-3, 8, 9); Vols. 3, 4 (all numbers); Vol. 5 (1, 6-8); Vol. 6 (1, 5, 7-12); Vol. 7 (1, 6); Vol. 8 (2); Vol. 9 (2); Vol. 11 (1); Vol. 12 (12); Vol. 14 (1, 5-6); Vol. 15 (4); Vol. 16 (2); Vol. 17 (1, 2); Vol. 18 (1); Vol. 20 (1, 2); Vol. 21 (2, 3); Vol. 22 (1); Vols. 23-26 (all numbers); Vol. 27 (1); Vol. 36 (1); Vol. 37 (2, 3); Vol. 38 (1). Volume groups 1-12, 13-18 and 19-44 contain 12, 6 and 3 issues respectively. Available issues of Vols. 1-6 $4.00, single issues 40 cents; Vol. 7 $2.50, single issues 25 cents; Vols. 8-12 $4.00, single issues 40 cents; Vols. 13, 14 $2.50, single issues 50 cents; Vol. 15 $3.00, single issues 60 cents; Vol. 16 $4.00, single issues 75 cents; Vol. 17 $5.50, Part I, $2.50, single issues $1.25. Subscription price per year $6.00.

Inquiries concerning exchanges for specimens, journals, special volumes or duplicate books should be addressed to *The American Midland Naturalist*, Notre Dame, Indiana, where subscriptions and payments are also received. Offers should accompany requests for exchange.

Abbreviated citation: *Amer. Midl. Nat.*

The American Midland Naturalist is indexed in the INTERNATIONAL INDEX.

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 45 JANUARY, 1951 No. 1

Notes on Nearctic Hepaticae

III. A Conspectus of the Family Lophoziaceae, with a Revision of the Genera and Subgenera[1]

Rudolf M. Schuster

Department of Botany, University of Minnesota,[2] Minneapolis

CONTENTS

Introduction 2
Historical summary 5
The limits of the family Lophoziaceae and its relationships 8
A critique of previous systems 13
Lophozia Dumort., emend K. M. 13
The Lophozia-Isopaches problem 13
The Lophozia-Leiocolea problem 15
The Lophozia-Tritomaria problem 16
The Lophozia-Barbilophozia-Orthocaulis problem 18
The L. excisa-Massula-Isopaches problem 20
Tritomaria Schiffn., emend. Buch 21
The Tritomaria-Lophozia problem 21
The Tritomaria-Jungermania quinquedentata problem 22
The Tritomaria-Saccobasis problem 24
Anastrophyllum Spruce, emend. Schuster 25
The Spenolobus-Anastrophyllum problem 25
The Sphenolobus minutus-Sph. saxicolus problem 25
The Sphenolobus-Crossocalyx problem 28
The Anastrophyllum-Orthocaulis problem 28
Synthesis of a new system of the Lophoziaceae 30
Keys to genera and subgenera 31
Phylogenetic key 31
Artificial (working) key to genera and subgenera 37
Treatment of individual groups 39
Lophozia Dumort., emend. K. M. 39
Subgenus 1. Orthocaulis Buch 40
Key to Nearctic species 42
Subgenus 2. Barbilophozia Lske., emend. R.M.S. 43
Key to Nearctic species 44
Subgenus 3. Leiocolea K. M. 45
Key to Nearctic species 47
Subgenera 4-6. Massula-Isopaches-Dilophozia: Introduction 48
Subgenus 4. Massula K. M. emend. R.M.S. 50
Key to Nearctic species 54
Subgenus 5. Isopaches Buch, emend. K.M. 56
Subgenus 6. Dilophozia K.M. emend. R.M.S. 57
Key to Nearctic species 58
Tritomaria Schiffn. emend. Buch 62
Key to Nearctic species (and subgenera) 65
Saccobasis Buch 65
Anastrophyllum (Spr.) Stephani 68
The Eurylobus-Euanastrophyllum complex 71
Subgenus 1. Eurylobus subg. nov. 71
Subgenus 2. Euanastrophyllum Schuster 72
Key to Nearctic species 72
The Sphenolobus-Crossocalyx-Eremonotus complex 72
Subgenus 3. Sphenolobus Lindb. emend. R.M.S. 74
Subgenus 4. Crossocalyx (Meyl.) Schuster 74
Temnoma Mitt. 75
Gymnocolea Dumort. 76
Anastrepta (Lindb.) Schiffn. 77
Mesoptychia (Lindb. & Arn.) Evs. 78
Acrobolbus G. L. & N. 81
Summary 82
References 88
Plates 90

1 The first paper in this series, *Dianthelia steerei gen. et sp. nova, a Critical Endemic of the Appalachians,* etc. appeared in The Bryologist 52: 101-120, 1949.

Introduction

The family Lophoziaceae represents the most polymorphic and difficult of the holarctic families of Hepaticae, as regards divisions into supraspecific groups. Within the last fifty years our concepts of classification have gradually shifted, and there has developed a tendency to divide the old genus *Jungermania* or *Lophozia* into numerous generic groups. The basis for such subdivision has varied from time to time. Loeske (1907) and Schiffner (1908) used the number of leaf-lobes; Müller (1910) introduced the use of the perianth-form; Buch (1933) extensively used the stem-anatomy; Müller (1939) then introduced the oil-body form. Whatever criteria were used, the inevitable result has been a gradual fragmentation of the old genus *Lophozia* into many smaller genera. With the use of different criteria, different systems of classification have resulted, most of them unfortunately at odds as regards some of the fundamental questions.

We have therefore arrived at the stage where a major effort at synthesis of the earlier systems, together with a new approach based on utilization of characters not widely used previously, is almost a necessary prerequisite for further work on the family. In addition, the following synopsis of the family includes keys to the Nearctic subgenera and species, since these are not given for the most difficult of the groups in the only American work treating the group (Frye and Clark, 1945).[3] The formal descriptions of the latter work, together with the summary of the ranges given, make any treatment of the species superfluous here.

The most recent review of the problem is the brief and generalized one of Andrews (1948), which appeared after most of the following paper was prepared. The review by Andrews is largely a critique of Buch's two systems

---

The second paper in the series, *The Hepaticae of the East Coast of Hudson Bay*, appeared as Bulletin 122, The Canadian National Museum (1950).

2 I would like to acknowledge the constant help of my wife, Olga M. Schuster, in the preparation of this paper, and of Miss Wilma Monserud, in the photography of the assembled plates. The illustrations are all originals, prepared by the author, largely from living materials. Part of the cost of reproduction of the plates has been defrayed by the Graduate School of the University of Minnesota; I would like to express my thanks to Dr. E. C. Abbe for making these funds available.

3 The treatment of the group in Frye and Clark (1945) cannot be followed, in many cases, because these writers frequently fail to draw any distinction between genetically determined characters (i.e., valid taxonomic characters) and phenotypic characters. Such environmentally controlled characters as relative thickness of cortical stem-cells are used to separate *Saccobasis* from other Lophozioid genera (p. 337). It is only necessary to compare pl. 25, fig. 9 (cortical stem cells of *Saccobasis*) with pl. 1, fig. 5 (cortical stem-cells of *Orthocaulis*) to see how little validity such a characteristic has. Again the presence or absence of pigmentation of the cell-walls is used in the generic key (p. 338) and specific keys (p. 380) but without any validity. In many of the species with normally whitish trigones or whitish cell-walls these may become yellowish or brownish under conditions of extreme insolation. *L. rutheana* (separated in the key on p. 380 by the hyaline cell-walls, *fide* Frye and Clark) for instance, may have them deeply golden-brown in color. In this respect, therefore, the treatment of Frye and Clark represents a decided regression from the relatively sound taxonomic traeatments of Buch (1933, 1936) and Müller (1910, 1939). See also the critique of the "Table of Comparisons" to *Lophozia*, and footnotes 34, 49, 57, 58, 77, 86.

(1933, 1942). Since it is felt that a critique rarely accomplishes more than the tearing down of a system, rather than substituting another, the following notes are published at this time. The purpose of this paper, therefore, will be to attempt a synthesis of what is acceptable in Buch's two published systems (1933, 1942) and the most recent concept of Müller (1939, 1940, 1947, 1948) and Meylan (1939), taking into account the other recent systems (Joergensen, 1934; Jensen, 1915; Casares-Gil, 1919, etc.).

At the outset I would like to express considerable agreement with what appears to be Dr. Andrews' main thesis: the *Lophozia-Sphenolobus* complex could well have been left as one genus, divided into numerous subgenera, these in turn into sections and subsections. It would seem, at this time, however, that such a treatment would find few followers, since it would result in a large heterogeneous, portmanteau genus. The tendency, not only in bryology, has been to split these large portmanteau genera into smaller ones: the ideal example being *Lejeunea* s. lat. Insofar as the segregates resulting are homogeneous and natural units, it would seem that a gradual shift in the value we adduce to the subjective term *genus* is of little consequence since that term, admittedly, is an abstraction and therefore subject to extremely different treatment at the hands of diverse workers.

On the other hand, it is desirable to use the term genus in a fashion that somewhat approaches consistency in any one group.[4] For that reason a re-evaluation of Buch's work seems called for since his "genera" are patently not the equivalent of most of the other genera now recognized in the bryophytes.[5] In addition, it is very probably true, as will be developed later, that some of his "genera" (*Isopaches, Sphenolobus, Lophozia*) are not entirely homogeneous units.[6] It would seem to the writer, however, that the only manner in which to attain a less subjective state of knowledge in the matter is by further critical work. Neither the review by Evans (1935), in which the groups are accepted without additional work corroborating Buch's data, nor that by Andrews (1948) in which these genera are rejected, also without any direct evidence being adduced, basically add anything towards a solution, except the *opinions* (however critical) of these workers.

For that reason the entire problem of the classification of the Lophozioid complex is re-examined here, and an attempt is made to integrate all the various philosophies and the characters they were based on, into one system. This is obviously not totally feasible, since some of the systems contain contradictory features. In these cases I have re-examined the problem and offered the conclusion which seemed most probably correct.

---

4 It would be naïve indeed to expect the term to be used in a semi-consistent manner in all plants and animal groups: the genus of *Lophozioid* species of Buch would be perfectly acceptable to most mammalogists, for instance, though quite unacceptable to some bryologists.

5 Such as *Mannia* (*Grimaldia*), *Riccardia, Plagiochila, Metzgeria.*

6 However much criticism Buch's systems may have resulted in, it must be admitted at once that they were the first truly dynamic systems set up, and, even if not acceptable, were of decided value in demolishing the entirely artificial distinction innovated by Stephani between "*Lophozia*" and "*Sphenolobus.*" However much we may object to details in Buch's systems, the above was not an inconsiderable virtue.

From such a synthetic effort emerges one major, obvious fact: it is extremely difficult to present a system that stands midway between the conservative one Andrews leans towards, or the radical one Buch has set up. The most obvious and easiest are these extreme solutions, for as Andrews expresses it, the retention of a single genus in the Lophozioid complex "would allow free play to the setting up of subgenera (etc.) according to the varied conceptions of different authors, without taxonomic harm and without adding unnecessarily to the already excessive burden of synonymy." Similarly, making a genus out of each species-complex (even if containing a single species), a system that Buch approaches, also does away with the problem of where to draw generic lines.

Neither of these solutions, though the simplest and most obvious ones to suggest themselves, appeal to the writer because the extraordinary difficulty of the complex does not appear to be resolvable by "easy" solutions. Furthermore, the day of portmanteau genera seems to be gone even though we may regret the consequent loss of the simplicity of the taxonomy of that period.

The difficulty that faces one in setting up a compromise scheme is obviously due to one factor, the extreme diversity in rank or standing[7] of the groups within the complex. Using genera, subgenera, and sections, we still have only three categories that we more or less arbitrarily "impose" on a system, in which there are obviously as many unequal categories as there are groups.

This may be illustrated as follows: Although I accept six genera (*Temnoma, Gymnocolea, Lophozia, Tritomaria, Saccobasis, Anastrophyllum*) in the *Lophozia-Sphenolobus* complex, they are of very unequal rank. *Temnoma* is probably the most isolated, followed by *Gymnocolea*. There is little doubt in my mind about the "separateness" of these categories as genera (as I define them here). However, I retain *Tritomaria* as a genus with misgivings, as distinct from *Lophozia*. Together with *Lophozia* it forms a well-definable unit, obviously separate from the other generic groups. Yet *Tritomaria* appears more strongly isolated than the "subgenera" within *Lophozia* I recognize. In other words, *Tritomaria* is a "Zwischenstuffe" between the generic and subgeneric categories (as accepted in this paper); it is recognized as a generic entity largely because its extreme members (*exsecta*, etc.) are so distinct, in spite of the fact that the intermediate member (*scitula*) so obviously bridges the gap between *Tritomaria* and *Dilophozia*. Similarly, within the old genus *Lophozia* there are a number of "subgenera," some of which, such as *Leiocolea*, are homogeneous units, separated by good characters and several "tendencies" that may be equally significant. In fact, if *Tritomaria* is separated as a genus from *Lophozia*, it is an academic question whether to recognize *Leiocolea* as a distinct genus or merely as a subgenus. On the other hand, some of the "subgenera," such as *Massula* and *Isopaches* grade into *Dilophozia*, forming a nearly continuous series.

It is obvious, therefore, that all types of categories exist in the complex, and that the basic problem is forever insoluble. Therefore, we are faced with two obvious solutions: call each of these categories genera, or place all of them into a portmanteau genus.

Although the latter perhaps is the most logical solution (since the former inevitably tends to result in as many genera as there are species or "Arten-Kreise"), it probably will no longer be accepted by the majority of students. We are therefore almost forced to look for a solution where our better sense

[7] The "rank" or "standing" being in direct proportion to the completeness of isolation from other groups.

tells us there is none, and then attempt to resolve what we recognize as the irresolvable.

The following system is an attempt at such a solution, however paradoxical it may seem to even make the attempt. The writer hopes, however, that the innate artificialities will be overlooked in favor of the obvious compromise that such an attempt offers, and the perhaps greater approach to a consistent generic treatment (as related to the treatment existing now in other groups) that it offers. It should be clear, from what has gone before, that total consistency (or even an approach to it) is patently impossible.

Historical Summary[8]

The earlier taxonomic views are discussed by Müller (1910), Evans (1935) and by Buch (1933), so need not be treated here. It may not be out of place, however, to state that much of the difficulty with the group has been due to acceptance of Schiffner's (1893) and Stephani's (1902) early division of the Lophozioid complex (excluding *Mesoptychia* and *Temnoma*) into two chief subgenera or genera: *Lophozia* and *Sphenolobus* (with *Anastrophyllum* considered a distantly related element). All writers, even Buch, have maintained *Sphenolobus* as a distinct genus. Müller and Macvicar retained it essentially in Stephani's sense (including such divergent elements as *Anastrophyllum michauxii, Tritomaria* spp., *Cephaloziopsis, Saccobasis, Crossocalyx,* as well as the species more lately restricted to *Sphenolobus*). The writer in the following essay will propose to do away with *Sphenolobus* as a genus entirely, following Buch in including some of its elements in the *Lophozia-Tritomaria* complex, while the few remaining species are placed within *Anastrophyllum.*

Buch (1933) divided the group into nine genera, *Lophozia, Leiocolea, Isopaches, Barbilophozia, Orthocaulis, Tritomaria, Saccobasis, Anastrophyllum* and *Sphenolobus* (leaving *Temnoma* and *Gymnocolea* out of the discussion.). This view was criticized both by Müller and Meylan (1939). Müller (1939, 1939-1940) at first was unwilling to accept *Isopaches* at all, even as a subgenus (following Meylan in this), and in addition he was unwilling to accept even *Saccobasis* and *Orthocaulis.* He also adhered to his earlier stand that *Barbilophozia* (incl. *Orthocaulis*) and *Leiocolea* were better treated as subgenera of *Lophozia.* Meylan set up the genus *Crossocalyx* for the anomalous species *Jungermania helleriana:* a species Buch had placed in his genus *Isopaches.* Meylan (1939) and Müller (1940) placed this genus into the Cephaloziaceae, a view which Buch (1942) attacked. Müller (1947) then came back to his earlier views and placed the genus into the Lophoziaceae, stressing the close relationship to *Eremonotus* and *Sphenolobus,* stating: "Vielleicht hätte man besser *Crossocalyx* und *Eremonotus* gar nicht zu beson-

8 Limitations of space necessitate restricting this discussion to the closely interdigitated *Lophozia-Sphenolobus* complex. In the case of the other generic groups there has been more agreement as regards their acceptance, in the literature.

dern Gattungen erhoben, sondern als Subgenera zu *Sphenolobus* stellen sollen."[9]

Buch (1942) offered an alternative, more conservative scheme, outlined as follows:

I. *Lophozia* (1. *Dilophozia*, 2. *Massula*)
II. *Barbilophozia* (1. *Orthocaulis*, 2. *Leiocolea*, 3. *Obtusifolium* (*L. obtusa*), 4. *Barbicaulis* (*L. barbata*) 5. *Barbifolium* (*hatcheri*, etc.)
III. *Isopaches* (*bicrenatus, decolorans, hellerianus*)
IV. *Tritomaria*
V. *Sphenolobus*
VI. *Anastrophyllum*
VII. *Saccobasis*

Group I is supposed to differ from Groups II and III in that it has a dorsiventrally differentiated stem medulla; from Group II in the lack of underleaves; from Group III in the thicker stem, etc.

As I have shown (Schuster, 1949) *Massula* has the medulla of the stem nearly or quite uniform (with the exception of *L. excisa*). Therefore there is no constant difference in this regard between Group I and Groups II+ III above. When one considers that *L. obtusa* (placed by Buch in II, by Müller in I) is so highly synthetic and intermediate, the value of a generic division between I and II becomes extremely doubtful. As will be shown later *Isopaches* (after excluding *hellerianus*) agrees very closely in most of its characters with *Massula* (stem structure; leaf-insertion; ♀ bracts; often paroecious inflorescence, etc.). The difference in stem-structure is the chief one relied upon by Buch to keep the group distinct from *Lophozia*. Since this criterion breaks down in the case of *Massula*, a separation between I and III becomes untenable, unless other characters are found. The 2-stratose capsule wall of *Isopaches* (contrasted to the 3-5 stratose wall of *Massula* and *Dilophozia*), and the presence of partly semi-annular thickenings in both the outer and inner walls of *Isopaches* represent more valid characters.

As is indicated elsewhere, a difference in one layer in thickness of the capsule wall can scarcely be considered a generic character in the Lophozioid complex (where it varies from 3-5 layers in the subgenus *Massula*, 3-5 in *Tritomaria*, 2-4 in *Anastrophyllum*, etc.). Furthermore, as Müller (1948, p. 9) indicates, the wall may rarely retain 3 layers in *L. bicrenata* which indicates that reduction to the bistratose condition is not yet completely fixed.

Even more significant than the lack of really important diagnostic characters, is the occurrence of so many synthetic forms that can be nearly as well placed in one subgenus as in another. *L. excisa, L. obtusa, T. quinquedentata, A. helleriana, Sph. saxicolus*, are a few of these "annectant" species, whose disposition into one group or another is at present a subjective matter. For that reason I preferred (1949) to associate Groups I-III into the single genus *Lophozia*, showing transition *only* to *Tritomaria* (through *T. scitula*); Groups V-VI are placed into another genus (which for reasons of priority must be called *Anastrophyllum*) while *Tritomaria* and *Saccobasis* are allowed to stand as in recent literature.

It is therefore evident that in spite of the recent, thorough review by Buch (1933), no final classification of the group has emerged. Furthermore, the more recent work by Müller (1939) on oil-bodies, Meylan (1939) on the position of *Crossocalyx*, Müller (1947) on the position of *Crossocalyx* and *Eremonotus*, and Müller (1948) on the capsule-wall, have all contributed to

9 Very recently Müller (1948) has swung to a more radical viewpoint, accepting almost all of Buch's groups, and allowing the following genera: *Isopaches, Lophozia, Crossocalyx, Leiocolea, Barbilophozia* (incl. *Orthocaulis*), *Tritomaria, Saccobasis, Sphenolobus, Anastrophyllum*.

Only *Orthocaulis*, of Buch's genera, is still unaccepted. The very varied viewpoints of Müller, over a period of a decade adequately indicate the extremely subjective nature of the generic classification of the group.

variously modify the conclusions of Buch. The revised classification first suggested by the writer (Schuster, 1949), based on a re-evaluation of the stem-anatomy as a criterion in classification, may therefore be used as a basis for the following classification, since it included at least a minimal amount of integration of the conclusions of Müller and Meylan.

Although the Lophoziaceae have been critically worked over recently by so many European students, there is nothing in the literature on the North American species of the family, with the exception of isolated notes on a few Nearctic forms by Evans (1893, 1896, 1900, 1902, 1903, 1912, etc.), and reviews of the work of Buch on the European members of the complex by Evans (1935) and Andrews (1948)—excepting only the treatment by Frye and Clark (1945), and scattered notes by Lorenz (1910, 1910a, 1911).

Frye and Clark (1945, pp. 337-442) follow Buch (1933) entirely as regards the generic limits employed. As pointed out in footnote 1, they unfortunately selected largely adaptive characters to separate some of the genera and the species. Their keys, therefore, are in part quite unreliable. In the most difficult of the complexes (*Lophozia*, sensu Buch) they do not attempt to construct a key. In addition, the treatment of Frye and Clark is also open to the same objections as the treatment by Buch. Unfortunately, though these workers accepted the divisions of Buch (founded essentially on presence or absence of differentiation of the medulla, and on the nature of the leaf-insertion), they do not once utilize the criteria on which the groups were established in their keys. For instance, though *Saccobasis* differs radically from the other generic groups in leaf-insertion (as has been pointed out for the last century by Nees, Meylan, Müller and Buch), they separate the genus because of the supposedly thick-walled cortical cells, even though such thickness is largely environmentally controlled, and in many cases so variable that no separation can be effected.

Though Frye and Clark follow the generic division of Buch they depart radically from Buch's concept (1933) on relationships as their table on p. 339 indicates. They (unlike Buch and the present writer) would derive the family from the Jungermaniaceae and indicate *Jungermania* as the ancestral type for the whole family! The "phylogenetic" sequences they draw include the following: *Jungermania* → *Lophozia* → *Orthocaulis* → *Saccobasis* → *Leiocolea* → *Isopaches*. Here there is supposed evolution from a form with entire leaves (*Jungermania*) and no underleaves; to a form with bilobed leaves and no underleaves (*Lophozia*); to a form with essentially 3-lobed leaves and distinct underleaves (*Orthocaulis*); to one with equally 3-lobed leaves and total lack of underleaves, and an extremely specialized stem structure (*Saccobasis*); to a group with bilobed leaves, distinct underleaves, an unspecialized stem-structure, but extremely specialized oil-bodies and perianth (*Leiocolea*); to a group with reduced stems, no underleaves, no specialization of perianth and oil-bodies (*Isopaches*). There are extremely few students of the leafy liverworts to whom such a "phyletic" arrangement would include any natural features. There is, for instance, the lack of logic in a series where there is supposed evolution from underleaf-free forms (*Jungermania, Lophozia*), to forms with underleaves (*Orthocaulis*) to forms with underleaves (*Leiocolea*) to forms that again lack underleaves (*Isopaches*). Similarly, there is hypothesized evolution from unlobed to bilobed, then to trilobed, and then again to bilobed leaves. There is believed to be evolution of forms with unspecialized oil-bodies (*Orthocaulis*) to forms with them very specialized (*Leiocolea*) to forms with them again unspecialized. There is supposed evolution from forms with specialized perianths (*Leiocolea*) to forms with them again unspecialized (*Isopaches*)! If the capsule-wall is taken as a criterion, similar lack of any consistent evolutionary pattern can be seen. A form like *Jungermania*, with a 2-stratose capsule wall gives rise to forms with it

3-5-stratose (*Lophozia, Orthocaulis, Saccobasis, Leiocolea*), and the latter give rise again to a form with 2-stratose capsule-wall (*Isopaches*). There is indicated evolution from forms with unspecialized medulla (*Jungermania*) to forms with it specialized (*Lophozia*) to forms with it unspecialized (*Orthocaulis*) to forms with the medulla and cortex both specialized (*Saccobasis*) to forms with both again unspecialized (*Leiocolea, Isopaches*)! The "Phylogenetic Diagram" of Frye and Clark can scarcely be said to embrace a logical and consistent treatment. The other developmental sequences drawn by these authors can be criticized in a similar fashion, and, to the writer at least, lack any acceptable elements. Frye and Clark (1945) also appear not to have seen the more recent papers by Müller (1939), Buch (1942) and Meylan (1939), which greatly modified the earlier system of Buch. Furthermore, Frye and Clark, in their keys made a number of erroneous generalizations (apparently on the basis of examination of the drawings in Buch, 1933) which are unfortunate, since they lead to numerous misdeterminations. It is therefore obvious that the little literature on the Nearctic members of the family needs to be supplemented by a critical study of the family, based on study of actual specimens (and, so far as possible, on the basis of *living* material). Since the writer believes that published keys to groups of organisms must, in all cases, be prefaced by actual study of all of the species in the group, an effort was made to obtain material of species not studied by Frye and Clark, especially those in North American herbaria.

The Limits of the Family Lophoziaceae and Its Relationships

I circumscribe, in the following notes, the Lophoziaceae essentially as in Joergensen (1934) and Müller (1940). The family, so circumscribed, represents a large share of the genera placed in the Jungermaniaceae or "Epigonianthaceae" (of the Buch, Evans and Verdoorn list, 1938; of Evans, 1939; of Verdoorn, 1932) (the rest being placed in the Jungermaniaceae, Southbyaceae, and Gyrothyraceae,[10] with two genera transferred to the Plagiochilaceae). As circumscribed, it essentially includes those genera in which the early ontogenetic lobing of the leaves persists into the mature state, and in which there is found a more or less terete (never strongly compressed) perianth, and oil-bodies formed of numerous minute spherules surrounded by a relatively firm membrane (i.e., not formed of several-many distinct globules), while the capsule-wall retains 3-5 cell-layers (with a very few exceptions).

The Lophoziaceae, as here circumscribed, include largely relatively un-

10 The Gyrothyraceae, nov. fam., constitutes an extremely isolated element. In Frye and Clark (1943) the species of this family are included in the Ptilidiaceae, in Evans (1939) in the Jungermaniaceae, in Buch, Evans, Verdoorn (1938) in the Epigonianthaceae, in Müller (1940) in the Nardiaceae. Although probably derived from a form similar to the Jungermaniaceae, the family differs from all Jungermaniaceae in a number of fundamental characters: a. The bistratose capsule-wall lacks all localized thickenings (again found only in the Porellaceae). b. The sporogonium is cylindrical, and is exserted from a tubular rhizoidous perigynium (much as in Calypogeiaceae), and further resembles that of the Calypogeiaceae in the linear sporogonium-valves, which are spirally twisted. If the Calypogeiaceae are retained as a family discrete from the Lepidoziaceae, the Gyrothyraceae obviously are fully as distinct from the Jungermaniaceae (in the same essential features). c. Large, obvious underleaves are retained. d. The rhizoids occur in dense, cushioned patches at the bases of the underleaves (see Howe, 1899). e. There is no perianth at all.

The inclusion of the only genus (*Gyrothyra* Howe) in the "Ptilidiaceae" by Frye and Clark (1943) is quite incomprehensible to the writer. The sporophyte structure, the spore-elater ratio, the succubous, entire leaves, and the rather small underleaves as well as the presence of a rhizoidous perigynium all are fundamental differentiating characters, that in their sum total, make any phyletic connection an extremely remote one at best.

specialized genera. The less advanced groups (*Lophozia* subg. *Orthocaulis*, *Temnoma*) are characterized by a suberect growth and an approach to the ancestral isophyllous condition, with the underleaves large and with retention of ventral stem-sectors about one-fourth the circumference of the stem in extent (1:6; 4:9)*. Associated with the unspecialized stem-structure, is retention of the primitive tendency to form deeply lobed leaves; there is further retention, in such "low" genera and subgenera as *Orthocaulis* and *Temnoma* of an apparently primitive lack of stability in leaf-lobe number: the two primary leaf-lobes exhibit a well-defined tendency to undergo secondary division (resulting in a maximum of four lobes) (1:6; 4:9); furthermore, there is a tendency in these groups for the leaf-bases to be ciliate (1:4; 4:1-6,9). In these characteristics the lower Lophoziaceae, in some measure, approach other "low" families of Jungermaniales: the Ptilidiaceae, the Lepidoziaceae, etc.

The Lophoziaceae, as a group, differ from the other groups that have been associated with them (Jungermaniaceae, Southbyaceae, Gyrothyraceae, Plagiochilaceae) essentially in lacking the innovations or specializations that these groups exhibit. Although perhaps not directly ancestral to these families, the Lophoziaceae possess features that make derivation of these groups, as well as the Scapaniaceae (and possibly the Marsupellaceae) from them (or near them) quite possible. The limits of the family can perhaps be best drawn from a comparison with these relatively specialized groups, as follows:

The Jungermaniaceae represent an advance over the Lophoziaceae in having acquired entire lateral leaves (with total suppression or reduction of the ventral or underleaves); they furthermore have their sporogonia-walls uniformly reduced to the bistratose condition (except for the "old" and somewhat annectant genus *Jamesoniella*). They retain the 2:1 spore-elater ratio, as well as the perianth-form of the Lophoziaceae, and are to be regarded as on the next highest developmental level above the Lophoziaceae. Conservative workers might well consider the Jungermaniaceae as merely a specialized offshoot or subfamily of the Lophoziaceae.[11]

---

* References of this type denote plates and figures throughout the present paper.

11 See in this connection the discussion under *Mesoptychia*. It should be stressed, however, that the Jungermaniaceae are difficultly derivable directly from the Lophoziaceae. They differ from them in almost uniformly lacking gemmae (occurring, rarely, in only *Jungermania lanceolata;* and here of a different form than found in Lophoziaceae). The Lophoziaceae almost uniformly are able to produce polygonal, characteristic gemma (smooth only in a few species of *Massula;* absent only in *Temnoma, Mesoptychia* and *Acrobolbus*).

There are several good reasons why a family separation between the Lophoziaceae and Jungermaniaceae is difficult to maintain. The lobed vs. entire nature of the leaves does not represent, in any way, an approach to an absolute criterion. In the Lophoziaceae there have been described, in recent years, species of *Anastrophyllum* with entire leaves; in other species of *Anastrophyllum* the sinus becomes very shallow, and the leaves are merely emarginate. Although these species are doubtfully referrable to *Euanastrophyllum,* and perhaps should be generically separated from *Anastrophyllum,* there can be no doubt that they belong, with *Anastrophyllum, Anastrepta,* and *Mesoptychia,* the Lophoziaceae approach or even attain the entire-leaved condition characteristic of the Jungermaniaceae. In addition, these advanced types (except for *Anastrepta*),

The Southbyaceae have advanced considerably over both Lophoziaceae and Jungermaniaceae in: having acquired opposite and entire leaves; a uniformly bistratose capsule-wall; development, throughout, of a well-developed perigynium; compound oil-bodies. There is, in some groups, a well-developed tendency to form restricted rhizoid-initial regions. The relationships of the family to the Lophoziaceae is obscure, but it retains the 2:1 spore-elater ratio of the Lophoziaceae.

The Plagiochilaceae, like the Southbyaceae, have compound oil-bodies (of the "grape-cluster" type), but the resemblance ends here: the leaves in various species retain the ability to develop marginal teeth or lobes (though species with 2-lobed leaves are very rare), and remain alternate; the spore-elater ratio remains 2:1; the capsule-wall (as in the Lophoziaceae) remains 3-7-stratose. Unlike all preceding groups, the perianth acquires a characteristically laterally compressed form.

The highly differentiated Gyrothyraceae have already been discussed (see footnote 10).

The Scapaniaceae appear to have been directly derived from *Anastrophyllum* or *Tritomaria*-like ancestral forms in the Lophoziaceae. Like the latter family, they retain a 3-7-stratose capsule-wall, uniformly bilobed leaves (with the dorsal lobe more or less smaller than the ventral), a generally 2:1 spore-elater ratio, and oil-bodies of the *Lophozia*-type (i.e., of numerous little or moderately distinct, scarcely protuberant oil-globules). They represent an advance over the Lophoziaceae in having acquired a complicate type of leaf, with the smaller dorsal lobe folded over the ventral, and generally separated by a discrete keel in the "folding-over" region. Furthermore, the perianths have become dorsiventrally compressed to a greater or lesser degree (unlike all previous groups). Though superficially very different in appearance, the fundamental characters separating the Scapaniaceae from the Lophoziaceae are relatively weak, and the family is not a sharply isolated one. The similar type of gemmae-formation also indicates a common origin.

The Marsupellaceae are of uncertain origin. Like the Lophoziaceae, the leaves remain bilobed (and like ancestral forms, somewhat transversely inserted), but become equally bilobed — a secondary feature; the cell-net is generally collenchymatous, but the oil-bodies become very large and few per cell (not unlike *Leiocolea*, however). As in some Lophozioid genera (*Anas-*

approach the Jungermaniaceae in their inability to develop gemmae. Furthermore, the less specialized Jungermaniaceae (which retain a 3-4-stratose capsule wall, or distinct underleaves), such as *Nardia geoscypha* and *Jamesoniella autumnalis* show a well-defined tendency to develop emarginate leaves.

Since the nature of the antheridia and antheridial stalks also appear to show no significant differences between the two groups, and since no significant differences occur between the two groups in the oil-body characteristics, the separation between the Lophoziaceae and Jungermaniaceae must be regarded as either one of convenience, or merely as a tentative one. It should be noted that some recent workers, counter to the rules of priority, use the term Nardiaceae for the Jungermaniaceae (Müller, 1940, etc.).

trophyllum, etc.) the ventral stem sectors are vestigial and develop no underleaves (*Gymnomitrium, Marsupella*) or retain minute ones (*Prasanthus*). Unlike most Lophoziaceae, the Marsupellaceae have nearly or quite lost the perianth. In the total absence of gemmae the group differs widely from the Lophoziaceae. Although not sharply definable on the basis of gross characteristics, the Marsupellaceae seem to be phyletically very distant from the Lophoziaceae, and are not clearly connected with that family.

It is evident, from the above outline, that the Lophoziaceae represent a highly synthetic group. They possess characters found in a relatively large group of families, and give evidence of occupying a position at or near the base, where these various families converge. The Lophoziaceae, in their "strategic" phylogenetic position, are therefore of considerable interest to the phylogenist.

The family may be formally defined as follows:

Family LOPHOZIACEAE

Gametophyte retaining the embryonic division of the enations (leaves) into two major lobes, in the mature state (1:1; 12:5); the "leaves" primitively in three rows, but the third row (underleaves) always moderately to highly reduced (4:9; 6:8) and lost in diverse groups (apparently independently) (12:5) the ventral stem-sectors correspondingly varying from a maximum of one-fourth the stem-circumference (4:9) to a minimum width of 1-2 rows of cells (18:2; 25:1). The gametophyte therefore distinctly bilateral and attaining a moderate to high degree of anisophylly. Dimorphism of axis absent; flagellae or stolons never produced. Leaves alternate, succubous (obliquely shingled) or transverse, with cells generally able to produce large, often bulging trigones under conditions of intense or moderate transpiration: usually more or less collenchymatous (2:7; 3:2) oil-bodies always present (without exception) simple (i.e., not compound), usually small or moderate in size (mostly 2.5-9 μ, only in *Leiocolea* becoming larger), several to many per cell (2:7; 6:4; 11:8). Rhizoids uniformly unicellular, the initial cells scattered haphazardly over the postical stem-surface (12:5; 15:6). Amphigastria moderate to minute, when present regularly retaining at least an indication of the bilobed ancestral type (1:6; 4:9; 5:4; 8:4). Leaves almost always retaining the ability to produce supplementary lobes (1:6; 4:7; 12:4-5), generally unable to produce marginal teeth, normally bilobed with the ventral lobe somewhat larger (18:2). Branching of two types: from endogeneous "buds," and axillary, from the lower halves of axils of normal vegetative leaves.[12] Vegetative reproduction usually present, normally by means of angulate, 1-2 celled gemmae produced on the leaf-lobes in branching fascicles (13:1; 14:6; 15:1); rarely by means of caducous perianths (26:1) never by means of caducous leaves or shoots, etc.

[12] I have also been able to demonstrate branching of a third type in *L.* (*Barbilophozia*) *hatcheri*, where a branch may replace the ventral half of a lateral segment (and lateral leaf), as in 7:2. However, axillary branching as in 10:1, 15:1, 20:6, 21:3 is much more frequent. Such branching also occurs in *Gymnocolea*.

Archegonia (and perianth) always terminal on main or long lateral shoots (5:1); androecia at first terminal on main or long lateral shoots, becoming intercalary by subsequent apical growth (17:2; 21:14).[13] Perianth present and generally free from bracts (in *Acrobolbus*, however, a perigynium present and perianth lost), typically cylindrical and inflated, with the apex more or less gradually narrowed and obtusely 4-5 (9-10) plicate (23:5), occasionally smooth and devoid of plicae (5:1; 26:1). Androecia with bracts subequal in size to normal leaves, similar to them but more or less saccate or ventricose at base, and often with an additional basal lobe or tooth on the antical margin; (21:12,15; 6:7; 17:2) bracts more transversely inserted than leaves, each with 1-3 short-ovoid antheridia (22:5; 21:15); paraphyses usually lacking; antheridia with stalks either biseriate or uniseriate (quite variable). Sporophyte with seta usually of unspecialized type: of numerous rows of cells (13:9; 14:4) but reduced to 4 inner, 8 outer rows of cells in some subgenera of *Anastrophyllum*. Capsule always short-ovoid, with wall generally of 3-5 layers of cells (in *Gymnocolea* and *Isopaches* becoming 2-stratose), mostly 20-50 μ thick, the inner wall usually with annular (i.e., radial plus tangential) thickenings, the outer with radial (nodular) thickenings only (6:1-2; 23:1-2);[14] valves lanceolate, not spirally twisted, dehiscing to base. Spore-elater (diameter) ratio always approximately 2:1 (6:3; 14:12; 23:4). Elaters usually bispiral, free.

The family, as so defined, would include the genera *Lophozia* (incl. *Orthocaulis, Barbilophozia, Isopaches, Leiocolea*, etc.), *Tritomaria, Saccobasis, Anastrophyllum* (incl. *Sphenolobus, Crossocalyx, Eremonotus*), *Anastrepta, Gymnocolea, Temnoma*, as well as (probably) *Acrobolbus* and *Mesoptychia* (though these genera, as will become apparent, are isolated from the others of the family), among the holarctic genera. Of the extraterritorial genera, *Cuspidatula* St., *Chandonanthus* Mitt., and *Hypogastranthus* Schiffn. are probably all to be included in the family (although several of these represent rather divergent elements). The following discussion will be based on study

13 Frye and Clark (1945: 342-343) attempt an artificial separation between species on the basis of whether the androecia are "terminal, just below the tip, or farther down the shoot," apparently not realizing that in the Lophoziaceae the apical cell is never used up in the formation of androecia, hence that androecia are not really terminal in almost all leafy liverworts. An androecium is always terminal when it is first developed, during the growing season, later becoming intercalary (as in 17:2); in many species there may be 2-3 androecia evident on the same shoot, the older ones from preceding seasons (as in 21:14, where an androecium is evident near the middle of the shoot, while near its base a portion of one is drawn, showing the male bracts of the preceding season). If one collects male plants of *ventricosa* early in the season they "key" to *ventricosa* in the table of Frye and Clark (pp. 342-343); if they are collected later, they appear to come out to *longiflora* (which is characterized by having the androecia "farther down the shoot"). It is apparent therefore that Frye and Clark not only use environmentally determined features in their keys (see footnote 3) but also use temporally controlled features.

14 In the reduced sporophytes of *Gymnocolea* and *Isopaches* the inner wall has the tangential bands reduced (*Isopaches*, 13:11) or virtually lacking (*Gymnocolea*); in other genera the median portion of the tangential bands are occasionally more or less obsolete (23:1).

of the holarctic genera only. It is probable that the major distributional region of the family lies in the North Temperate to Arctic-Alpine Zone; Tropical and South Temperate forms are relatively few.

A Critique of Previous Systems[15]

LOPHOZIA Dumort., emend K. Müll.

I find, after critical study, that the circumscription of the genus *Lophozia*, as given by Müller (1910, p. 659, and 1939, p. 341) is more natural and satisfactory than that given by Buch (1933, p. 284). My reasons may be outlined in the following manner:

THE LOPHOZIA-ISOPACHES PROBLEM

1. Buch separates *Isopaches* because of the smaller stem which is only about 8 cells high (13:8) vs. 10 cells or more high in *Lophozia*, sensu Buch (17:8; 14:7).[16] With reduction in size of a species, such reduction in number of cells is to be expected, and, in my estimate, of little phyletic significance unless extreme and sharply separated from the parent type. On the basis of the stem size *Lophozia gracillima*, with the stem 9-10 cells high (15:5,7) could go into either genus.

2. *Isopaches* is supposed to differ from *Lophozia* (sensu Buch) in that the growth is ascending or erect with gemma formation. This also holds for *L. gracillima* and *longidens*.

3. *Lophozia* (s. Buch) is supposed to differ from all other Lophozioid groups (except *Tritomaria* and *Saccobasis*) in that the medulla of the stem shows dorsiventral differentiation, the upper part consisting of larger, more elongate cells, the lower of shorter, narrower cells (17:8; 14:7; 15:7). Buch follows Jensen (1915, p. 116, 119, 123) in dividing the genus (as he delimits it) into three sections, the *Ventricosae* (including *ventricosa, porphyroleuca, wenzelii, alpestris, silvicola, longidens* and *gracillima*), *Excisae* (including *excisa, elongata, mildeana, marchica, jurensis*), and *Incisae* (including *incisa* and *grandiretis*). As I have shown (Schuster, 1949) and as is evident from the drawings (10:9; 11:5; 12:1) the stem of *L. marchica* (Sectio *Excisae*) and of *L. grandiretis* (Sectio *Grandiretae*) show none of the peculiarities that Buch has stressed as the chief generic character of the genus *Lophozia*, emend. Buch. It therefore follows that his diagnosis of the genus was based largely on the Sectio *Ventricosae* (of which he has figured *L. gracillima* and *silvicola*)

With the demonstration that the stem structure used as the chief criterion by Buch (1933, 1942), and which Buch has used (1942) to defend his posi-

15 In this section the various categories (and the manner in which they were circumscribed) are critically examined in detail. In view of the diverse opinions which have been expressed regarding their standing and limits, such a critique appears a necessary preliminary to the synthetic effort in Section V. *Gymnocolea, Temnoma* and *Acrobolbus*, etc. are not treated here, since they pose no special problems.

16 In my experience *L. bicrenatus* may have the stem 9-10 cells high, while Müller (1948) reports the stem of *L. decolorans* as 10 cells high.

tion, does not separate *Lophozia* emend. Buch from the other genera, it becomes obvious that *Lophozia* emend. Buch is not a natural group. If *Isopaches* is separated from it because of the stem structure, and that appears to be the chief reason for separating it, then it becomes evident that *Isopaches* is not a well established genus, even after *hellerianus* is separated from it, as done by both Müller and Meylan (which I find I must follow).[17]

4. Finally, I am convinced that the position of *"Isopaches" hellerianus* is not near *Lophozia,* but near *Sphenolobus minutus,* from which I think Meylans' genus (*Crossocalyx*) is no more than subgenerically distinct. The reasons for this are given in detail when the classification of the *Anastrophyllum* complex is discussed.

5. Buch (1933) also separates the genus because of the reduced seta (i.e., not of the "General type" of Douin, 1908), with it reduced to a finite number of cells (either 4 inner and 8 outer, or with a third layer of 16 outer cells). In 1942 (p. 293, Fig. 1:6) he shows two cross-sections of the seta of *I. bicrenatus,* in both cases with a finite number of epidermal cell-rows (16), but with the inner number of cell-rows infinite. In my experience the number of cell rows is even more indefinite, since not only the inner basic four cells may divide by periclinal walls (as Buch stresses), but also the outer layer, which may have a variable number of external rows of cells (20, for instance, in 13:9). *Isopaches,* therefore, cannot be said to differ sharply from other groups in the structure of the seta, since the seta is of basically the same type as in *Lophozia* (compare 14:4).

6. Müller (1948) attempts most recently to keep *Isopaches* separate, largely (apparently) on the basis of the type of thickenings of the capsule wall and the number of layers of the capsule-wall. *Isopaches* is placed in a type by itself, as regards the capsule-structure (Type c, p. 7), because the outer layer and inner layers are both supposedly provided with semiannular thickenings. This difference is not as striking as it appears on paper. In many species the outer capsule-wall has the radial thickenings extending more or less onto the tangential walls (as in 23:2), approaching the development of semiannular thickenings (compare 23.2 with 13:10). Again, many species have the median portion of the tangential bands of the inner capsule wall partially obsolete (as in a few cases in 23:1), while in *Isopaches* this condition has become merely more extreme (13:11), although a fair percentage of tangential bands remain complete. Furthermore, in *I. bicrenatus* the capsule-wall is frequently 3-stratose (and is described as such in Frye and Clark, 1944: 374). Müller (1948, p. 9) also describes the capsule wall of *I. bicrenatus* as bistratose ("rarely 3-stratose").

Summary.—The separation between the genus *Isopaches* (after removal

17 Buch also uses as a generic character the equally thick-walled leaf cells (i.e., their non-collenchymatous nature) (13:3-4). This again offers no separation. In most species of the sections *Excisae* and *Incisae* the leaf-cells also lack ability to develop trigones, and in such species as *Lophozia grandiretis* the leaf cells may become rather strongly thick-walled, with no distinct trigones developed.

of the foreign element *hellerianus*) from *Lophozia* is not warranted, since there is no sharp difference in the type of stem structure, nor in the leaf-cells, and since the difference in height of the stem is correlated largely with differences in the total size of the plants.

Study of the oil-bodies (Müller, 1939) shows that their size and number correspond closely to those of *Dilophozia* (i.e., the sectio *Ventricosae* of Buch and Jensen). However, the stem structure is most similar to that of the Section *Incisae* (which Müller has placed in the subgenus *Massula*), in which there are more numerous and smaller oil-bodies (11:8; 12:7). It seems to the writer then, that *Isopaches* with its two species (*bicrenatus, decolorans*) represents in some manner a link between *Dilophozia* and *Massula* (Müller, 1939, emend. Schuster). It seems scarcely warranted to retain a generic name for two species that appear to stand nearly midway between two subgenera. See in this connection also the discussion of the subgenus *Isopaches*.

THE LOPHOZIA-LEIOCOLEA PROBLEM

Although *Leiocolea* is certainly a more discrete entity than *Isopaches*, the writer feels that it is still better treated as a subgenus of *Lophozia* (see K. Müller, 1910) for the following reasons:

1. Buch (1933, p. 288) states: "Die gut charakterisierte Untergattung *Leiocolea* habe ich zur selbstandigen Gattung erhoben weil sie auch noch im Stammbau von *Lophozia* abweicht." *Leiocolea* (5:8) has a uniform medulla of the stem in apparently all species (which I believe to be the primitive condition). Since, however, I have shown that both *Massula* and the subgenus *Isopaches* (of which the first was retained by Buch in *Lophozia*) have a stem structure that is nearly identical with that of *Leiocolea* (compare 9:8; 10:9; 12:1; 13:8), it follows that the reason cited by Buch for elevating *Leiocolea* to the rank of a genus does not exist.

2. I find that in *Leiocolea* (unlike almost all species of *Dilophozia, Massula, Isopaches*) the cuticle is very generally strongly papillose (5:3) much as in the subgenus *Orthocaulis* (1:2), with which Buch correctly indicated a relationship. This also seems to indicate the subgenus is a discrete entity. Furthermore, Müller (1939, p. 341) has shown that the oil-bodies of *Leiocolea* (see 5:3; 6:4,5) are of characteristically large size, and few in number in each cell. These two characters, together with the perianth form (5:1; 6:6) almost suggest that *Leiocolea* be given the rank of a genus (in spite of the fact that the difference in stem structure cited by Buch does not exist). However, the anomalous species *L. obtusa* (which Buch placed in *Leiocolea*, Müller [1939] however now places in *Massula*) indicates a generic separation perhaps unwise. *L. obtusa* may have a weakly papillose cuticle and nearly horizontal leaf-insertion, like *Leiocolea*, but has the perianth of *Massula* and, of more importance, the numerous small oil-bodies characteristic of *Massula*. Since this species superficially appears to form a link between the two groups, it may be attempted to derive *Leiocolea* from the primitive subgenus *Massula*, from

near *L. obtusa*.[18] The anomalous character of *L. obtusa* has led Buch (1942, p. 289) to place it in a separate subgenus (*Obtusifolium*).[19]

3. Buch also stresses the fact that in *Leiocolea* the "Seitenblattfläche und-insertion [ist] der Stammlängsachse fast parallel." Although this is true as a generality, and is correlated with a very horizontal mode of growth (with the shoot tips nearly horizontal scarcely ascending) it does not hold for *L. heterocolpa*, in which the shoots (whether gemmiparous or gemmae-free) may be ascending to suberect (especially where crowded), and where the leaves are obliquely inserted and are in a plane at an oblique angle with the stem. Buch stresses this elsewhere (as for instance in separating the genus *Orthocaulis* from *Barbilophozia*), as a generic character. It would seem that a similar divergence in one group is as important as in a related group. I do not consider *L. heterocolpa* as other than an anomalous species of the subgenus *Leiolea*, and cannot consider a difference in mode of growth (whether ascending or horizontal) as of generic significance, by itself.[20]

Summary—*Leiocolea* agrees with the subgenus *Massula* of *Lophozia* in the essential stem structure. It therefore follows that the separation of *Leiocolea* from *Lophozia* by Buch (1933, 1942), on the basis of stem structure, is not warranted. *Leiocolea* further includes several divergent elements (*heterocolpa, rutheana*), which are almost as different from *Leiocolea* (s. str.) as the latter is from *L.* (*Massula*) *obtusa*. The most important separating character is that discovered by Müller: the very large oil-bodies of *Leiocolea* which occur only 2-4 per cell. Though more isolated than the other subgenera I place in *Lophozia*, *Leiocolea* superficially appears to be connected with the *Massula-Barbilophozia* complex by the anomalous and highly synthetic species *L. obtusa*.

THE LOPHOZIA-TRITOMARIA PROBLEM[21]

Buch (1933, p. 296-297) has unquestionably done a great service in calling attention to the fact that *Lophozia* (but only the Sectio *Ventricosae!*) is closely related to *Tritomaria*.[22] He states: "*Saccobasis* und *Tritomaria* sind vielleicht aus *Lophozia*-artigen Vorfahren entstanden und haben sich in verschiedene Richtungen stark differenziert." Buch apparently based this hypothesis on the similarity in stem structure between *Lophozia* (Sectio *Ven-*

18 The reasons why this lacks phyletically valid logic will be considered later. In the discussion of *Massula*, p. 52, the problem of the relationships of *L. obtusa* are discussed in some detail, and it is hoped its position clarified.

19 I find this subgenus unnecessary, for reasons cited on p. 53.

20 The relatively broad ventral stem-sectors of *Leiocolea* may be cited by some as indicating a separation from *Lophozia*. However, in *Lophozia* subg. *Massula* they are equally wide (see 12:5; 9:4).

21 See also p. 21.

22 Meylan (1924), however, had already discussed the close relationship between *Lophozia* and *Tritomaria*.

tricosae only!) and the two groups in question. In addition, the following are other similarities I would like to cite:

1. The cells in both the *Ventricosae* and *Tritomaria* are strongly collenchymatous under conditions of moderate to strong transpiration (compare 24:4 and 22:11 with 15:3; 17:4).

2. The rhizoids form an equally dense mat in both groups (compare 24:1 with 18:4; 15:6).

3. Underleaves are quite absent and the ventral stem-sectors are equally reduced in both groups (compare 18:2 with 24:2).

4. The perianth is similar (compare 17:1 with 23:5).

5. *L. ventricosa* and its allies very often produce nearly equally 3-lobed leaves, and fertile shoots may have most leaves of such a type (note 3-lobed leaf in 15:6, right). In *Tritomaria scitula* the leaves are regularly 3-lobed, with all lobes subequal (22:7,10). Occasional 2-lobed leaves, however, occur (22:12). In my estimation *T. scitula* stands nearly midway between *Lophozia* and *Tritomaria*, and if placed in *Tritomaria* (to which it is certainly very closely allied) renders the asymmetrical leaf-form of little value as a generic character. There thus seems evident a direct evolutionary sequence as follows: *Dilophozia* → *T. scitula* → *Tritomaria* s. str.

This absence of a sharp separation in leaf-form suggests that *Tritomaria* might be better treated as a subgenus of *Lophozia* (s. lat.). Indeed, I cannot see a greater difference between *L. longidens* and *T. scitula* than a subgeneric one, at best. However, *Tritomaria* has been considered by nearly all workers as a discrete genus. Furthermore, it may prove desirable to include in it (as a subgenus) the anomalous *Saccobasis politus*. It may therefore be advantageous to separate *Tritomaria* as a genus, including *Saccobasis*, to be derived from near the subgenus *Dilophozia*.

The differences in leaf-insertion between *Dilophozia* and *Eutritomaria* on one hand, and *Eutritomaria* and *Saccobasis* on the other hand, do not impress me as of more than subgeneric nature. In the suberect growing *L. longidens* and *L. gracillima* (15:1) the ventral half of the leaf is quite obliquely inserted (15:6), the dorsal half nearly transversely so; furthermore, the leaf approaches the canaliculate form typical of *Tritomaria*. A shoot of *L. gracillima* or of *longidens* with some leaves 3-lobed looks scarcely different from one of *T. scitula*. Furthermore I find *T. scitula* frequently produces shoots with some leaves 2-lobed (22:12). Also, the angle of insertion of the leaf is modified appreciably by the mode of growth — a fact Buch appears to overlook. In the somewhat ascending *T. exsectiformis* and *exsecta*, etc., the insertion approaches nearer a transverse one than in the more decumbent growing *T. quinquedentata* (24:1-2,7). Similarly, the suberect growing *L.* (*Dilophozia*) *longidens* and *gracillima* have the dorsal half of the leaf virtually transversely inserted (15:1) while the decumbent growing *L. ventricosa* and allies have it more distinctly oblique (16:4, etc.). Crowding of leaves has

the same effect: in mod. *densifolia* of *ventricosa* and *porphyroleuca* the leaves become much more nearly transversely inserted. Which condition one is to consider "normal" here is too subjective a question for the writer to attempt to answer.

The predominance of 3-lobed leaves in *Tritomaria* and the more nearly transverse insertion of the leaves, together with their approach (in most species) to a canaliculate condition and the generally strongly papillose leaf-cuticle, appear to be the only characters in which the group has advanced over *Lophozia* subg. *Dilophozia*.[23] The perianth form, thickness (in cell-layers) of the capsule-wall, the gemmae-form, stem-structure, form and number (per cell) of the oil-bodies, and their size, are identical in both groups. The two genera are certainly extremely closely related, and *Tritomaria* is best placed after *Dilophozia*. Its inclusion within *Sphenolobus* was certainly an extremely artificial feature of earlier classifications.

THE LOPHOZIA-BARBILOPHOZIA-ORTHOCAULIS PROBLEM

Buch (1933, 1942) separates *Barbilophozia* and *Orthocaulis* from *Lophozia* because of a difference in stem structure that I have shown does not exist. *Barbilophozia* and *Orthocaulis* both have the medulla of the stem of uniform cells, or nearly so, with little or no dorsiventral differentiation (1:5; 7:1; 8:6,11). Since this is also the case in *Lophozia* subg. *Massula* (9:8; 10:9; 12:1), I cannot follow Buch (1942) in separating a genus *Barbilophozia* or two genera (*Barbilophozia* and *Orthocaulis*).

Buch, I believe correctly, stresses that *Orthocaulis* shows a distinct relationship to *Temnoma* and *Leiocolea*. It is also undoubtedly allied to *Barbilophozia* (perhaps through *floerkii*). In spite of the fact that the stem structure offers little or no help in attempting a separation between the Lophozioid groups (with 2-lobed leaves) and the *Orthocaulis-Barbilophozia* complex (with mostly 3-4 lobed leaves), there is still little direct connection between them. However, *L. obtusa* stands superficially midway between *Orthocaulis* (where it was placed by Müller, 1910) and *Massula* (where it was placed by Müller, 1939) and *Leiocolea* (where it was placed by Buch, 1933), while it also shows a distinct relationship to *L.* (*Barbilophozia*) *barbata* (emphasized by Meylan, 1939). To what degree some of these apparent relationships are due to convergences can scarcely be answered without evidence of a more fundamental nature; but the highly synthetic nature of the species sufficiently emphasizes the fact that "generic" lines in the entire complex can scarcely be said to exist on a morphological basis. Buch has similarly shown that there is a gradual connection from *Orthocaulis kunzeanus* to *Temnoma* (through *O. quadrilobus*), while I believe that the presence of occasional postical basal leaf cilia in *Leiocolea rutheana* also suggests that *Leiocolea* may be derived from the

[23] However, in *Tritomaria* (and more strikingly so in *Saccobasis*) there is a well-developed tendency for the basal leaf-cells to become elongate (22:3; 25:10) and for the dorsal cortical stem-cells to be narrow and long (22:2; 25:9); the stem cells also average narrower than the basal leaf-cells, unlike *Dilophozia*.

Orthocaulis-Barbilophozia complex (but from nearer *Barbilophozia* than *Orthocaulis,* rather than directly from *Orthocaulis,* as Buch (1933, p. 294, 296) insists). The weakest point in the diagram illustrating phyletic relationships given by Buch (1933, p. 296) is the linear series: *Orthocaulis* → *Leiocolea* → *Barbilophozia.* This seems very unconvincing to the writer, and apparently followed from the concept that the archetype had a fixed 2-lobed leaf. As I will show in my summary (p. 82) the archetype probably had a leaf with the lobing very unstable, varying from 2-4-lobed, depending partly on nutritional factors (which is still the case in *Orthocaulis* and *Barbilophozia* to some degree). From such an archetype *Barbilophozia* arose by an increase in dorsiventrality, and from near its base arose *Leiocolea* by the development of genetically fixed 2-lobed leaves. Therefore, the sequence should be nearer *Orthocaulis* → *Barbilophozia* → *Leiocolea.* Certainly the perianth form would suggest placing *Leiocolea* at the extreme since this is unmodified in both *Barbilophozia* and *Orthocaulis.* The very specialized nature of the oil-bodies also suggests it represents a sidewise specialization (while *Barbilophozia* and *Orthocaulis* agree in the relatively unspecialized nature of the oil-bodies). This concept of relationships is more fully brought out in the summary (see Diagram I).

That *Barbilophozia* and *Orthocaulis* are closely related has not been challenged by anyone. Even Buch (1942) in a less extreme scheme unites *Orthocaulis* and *Barbilophozia* in the genus *Barbilophozia.* However, Müller does not accept *Orthocaulis* at all, which in my estimation, is worthy of subgeneric recognition for the following reasons:

1. The leaf-insertion is less oblique in *Orthocaulis* (compared to *Barbilophozia*) and the number of leaf-lobes less "fixed" genetically: indicating a less specialized group (compare 2:4 and 3:1 with 8:1,5,9).

2. The growth is suberect or at least ascending; in *Barbilophozia* very characteristically horizontal, unless crowded.

3. The highly synthetic nature of *Orthocaulis* makes it desirable, purely from a practical point of view, to separate it nomenclatorially from the obviously side-wise specialized *Barbilophozia.*

Summary.—Since *Barbilophozia* and *Orthocaulis* agree in the uniform stem-medulla with *Lophozia* subg. *Massula,* any attempt to separate them from *Lophozia* on the basis of stem anatomy is invalid. Furthermore, both groups have the same type of oil-bodies (and nearly same size and number per cell) as *Dilophozia,* while the perianth-form, leaf-insertion, gemmae-form, collenchymatous cell-net, etc., all agree with *Dilophozia* in their general features. This suggests that some form midway between *Massula* and *Dilophozia* was closely related to (and probably derived from) some form near or ancestral to *Orthocaulis.* The derivation from such an ancestral form would entail chiefly the obsolescence of the ventral stem-sectors (and consequent loss of underleaves), and the development of a genetically fixed bilobing of the leaf.

Therefore, if *Barbilophozia* (incl. *Orthocaulis*) is separated at all from *Lophozia* in any generic sense, it must be done on the basis of retention of underleaves and the 3-4-lobed leaves. Since the less specialized species of *Orthocaulis* (such as *kunzeanus*) have predominantly 2-lobed leaves, while other species (such as *attenuata*) have lost their underleaves, there is scarcely any sharp distinction between *Lophozia* s. str. and *Barbilophozia* (incl. *Orthocaulis*). The less modified species are so close that a generic separation appears futile.[24]

THE L. EXCISA-MASSULA-ISOPACHES PROBLEM

With the demonstration that the stem-anatomy offers no sharp distinction between *Lophozia* (including *Massula*) and *Isopaches*, the question is immediately raised as to whether or not there is sufficient difference between *Massula* and *Isopaches* (both of which have the stem with a uniform medulla) to warrant their separation.

There is but little doubt that *Massula* superficially approaches *Dilophozia* (through *perssonii* and *excisa*). Similarly, *Massula* superficially approaches *Isopaches* (through the *excisa-perssonii* complex and through *I. bicrenatus*). In fact, the subgeneric limits of these groups are quite unsatisfactory as at present defined in the literature. *Dilophozia* includes species with a specialized medulla; *Massula* includes species predominantly with the medulla unspecialized (but distinctly specialized in the *excisa-perssonii* complex); *Isopaches* includes only species with a simple medulla. It is apparent from this that if we are to retain the medulla-character at all as a significant character, we cannot retain *Massula* as originally circumscribed by Müller (1939) and accepted by Buch (1942). The question then is whether to take the *excisa-perssonii* complex (which has the stem of *Dilophozia*, but otherwise approaches *Massula*) and place it in a new subgenus, whether to leave it in *Massula*, or whether to take it as evidence that *Massula* and *Dilophozia* should be reunited.

Müller (1939) has done an unquestionable service in the clarification of the Lophozioid complex by using the oil-body characters in the separation of subgenera in *Lophozia* (*Massula* and *Leiocolea*). An objective student, however, can scarcely see why *L. excisa* should go into *Massula*, while *L. silvicola* should go into *Dilophozia*. The first (14:2) has anywhere from 7-18 oil-bodies per median leaf-cell; the latter (16:5,8) mostly from 15-25. There is little doubt but that the two subgenera grade into each other on the basis of oil-body size and number — the chief criterion used by Müller. If we, however, use the structure of the oil-body as the basic criterion, a more natural classification merges. In *Massula* (10:7-8; 11:8; 12:7) the oil-bodies are relatively homogeneous, without appearing to be made up of a large number of oil-spherules; they are therefore smooth externally, and appear very highly

24 The species of *Barbilophozia* (such as *barbata* and *attenuata*) that have obsolete or no underleaves have admittedly lost them independently of the species of *Lophozia*. Hence the phyletically most significant difference between *Barbilophozia* (s. lat) and *Lophozia* (s. str.) lies in the retention of underleaves in almost all species of *Barbilophozia* (and general retention of cilia of the postical leaf-bases).

refractive. Furthermore, these oil-bodies persist in such a form for a considerable time in dry material, without undergoing disintegration into numerous finer oil-globules.[25] In *Dilophozia* (and in *L. excisa*) the oil-bodies consist very obviously of a variable and large number of included oil-globules, which appear to protrude slightly through the common containing membrane, resulting in more or less papillose or granulose-appearing structure (14:2; 16:3,5,8; 17:4). In material that has been dry for more than 3-6 months these oil-globules generally are released when the plant is soaked in water, apparently by the disintegration of the common surrounding membrane, and a large number of oil-spherules are present in the cell, all of these in more or less active Brownian movement. The distinctness of the included oil-globules within the oil-bodies is apparently a variable, appearing to increase with either age of the cells or with time the plants have been allowed to dry.[26]

Since *L. excisa* (and the related *L. perssonii*) have the stem-structure of *Dilophozia*, while their oil-bodies are also similar to that subgenus, I propose to place the *excisa-perssonii* complex into *Dilophozia* (as the Sectio *Excisae*).

Since *Massula* as circumscribed by Müller (1939) and Buch (1942) is not a homogeneous group, and since *Isopaches* as circumscribed by Buch (1933, 1942) is also heterogeneous, the classification of this entire complex, which I feel certain is closely interrelated, is in very unsatisfactory state, in the literature. The writer's viewpoint regarding its classification is given on page 48.

Summary.—Massula K. Müller includes elements with a homogeneous medulla (these I would regard as typical *Massula*), and several species (*excisa, perssonii*) with a dorsiventrally differentiated medulla, the ventral band of which is attacked by mycorrhiza (much as in *Dilophozia*). The latter, in my estimation, are not to be retained in *Massula*. Similarly, *Isopaches* (as defined by Buch, 1933, 1942) includes elements that are distantly related (*hellerianus*, which is better placed in *Anastrophyllum*, s. lat.; and the *bicrenatus-decolorans* complex). The latter complex, in my estimation, belongs in *Lophozia* (although Müller, 1948, also now excludes it from *Lophozia* generically), and is closely related in most respects to *Massula*.

TRITOMARIA Schiffner

THE TRITOMARIA-LOPHOZIA PROBLEM

As is indicated on p. 17 there is no major break between the less derivative species of *Dilophozia* (such as *longidens*) and the less derivative species

25 I have examined material of *L. marchica* collected three years before, in which the somewhat ovoid, minute, homogeneous oil-bodies persisted, in many cells, without undergoing dissolution into oil-spherules. In *L. obtusa* I have also seen material, almost ten years old in which some cells retained distinct oil-bodies, which also did not undergo disintegration into oil-spherules.

26 It is therefore possible that in some of the accompanying drawings the included oil-spherules appear much more distinctly defined than in actual preparations from living leaves. Some of the oil-body drawings have been based on material which had been dry for as long as 6-9 months.

of *Tritomaria* (such as *scitula*). In all probability the entire complex (including *Saccobasis* and *Trilophozia*) is to be derived from such a *Dilophozia*-like form.

Since, however, it is probable (as Buch also indicates) that *T.* (*Trilophozia*) *quinquedentata* and *Saccobasis polita* share a common ancestral form with *Eutritomaria*, it becomes almost a necessity to separate *Tritomaria* generically. Since the genus includes these divergent subgroups, or subgenera, I believe we have almost no alternative. Furthermore, there is no species in *Dilophozia* that regularly produces trilobed leaves, while the species of *Tritomaria* (s. lat.) produce bilobed leaves only occasionally (in all species except *T. scitula* associated with gemmae formation).

Except for the tendency towards development of extremely asymmetrical leaves (which is nearly absent in *scitula* and *polita*), the genus differs from *Lophozia* only in the genetic fixation of a 3-lobed leaf, and the retention of a dorsally transverse type of insertion. The nearly transverse type of leaf-insertion is one of the strong arguments in favor of retaining *Tritomaria*. Since both dorsal and ventral halves of the leaves have become quite obliquely inserted in all species of *Dilophozia* (less so only in the *longidens-gracillima* complex), it becomes difficult to derive the nearly transverse-leaved *Tritomaria* from *Dilophozia*. This is largely so because nearly transversely inserted leaves are to be considered primitive. We are therefore constrained from deriving *Tritomaria* directly from *Dilophozia, but* rather from a common ancestral form.[27]

THE TRITOMARIA-JUNGERMANIA QUINQUEDENTATA PROBLEM

The disposition of *J. quinquedentata* has remained somewhat unsatisfactory. Buch (1933) was the first to place it in *Tritomaria*, and was followed by Evans, Verdoorn, Frye and Clark, and Müller (1939), but was criticized for this by Meylan (1939). Meylan, apparently, still inclines to the older view that the species is related more nearly to *Barbilophozia*. Buch (1942) correctly stresses the fact, however, that the stem-structure of *T. quinquedentata* approaches nearer the *Tritomaria-Dilophozia* type (i.e., shows a dorsi-ventral differentiation) (compare 24:5 with 22:1, 17:8). Furthermore, the total lack of underleaves and narrow ventral stem-sectors (24:2) are features that do not occur in *Barbilophozia*: nor do asymmetrically trilobed leaves. Finally, the leaves of *J. quinquedentata* have the dorsal end of the insertion virtually transverse, though in much material not as absolutely as in *T. exsecta* (24:7).

The leaf form, narrow ventral stem-sectors, stem-anatomy, all indicate that

---

27 However, in the Section *Longidentae* of *Dilophozia* the leaves may be nearly transversely inserted dorsally (15:1), and approach *Tritomaria* (22:7-8). The separation between the two genera, on this basis, is therefore also extremely difficult to maintain.

the disposition by Buch is correct. Any resemblance to *Barbilophozia*, is, I believe, entirely due to convergence.[28]

However, as Müller points out in 1948, *T. quinquedentata* is not closely related to *Tritomaria* s. str. (as exemplified by *T. exsecta*). According to him, the capsule-wall is 5-stratose in *T. quinquedentata* (3-stratose in *exsecta*), and the antheridial stalk consists of two rows of cells (1 row in *exsecta*). These differences are rather fundamental.[29] Furthermore, *T. quinquedentata* differs in vegetative characters from *Tritomaria exsecta* as well: the leaves are more strongly spreading, with the entire line of insertion (except the dorsal tip) rather oblique (24:1,2,7); the leaves scarcely concave and not or little complicate-canaliculate; the sinuses between the ventral lobes as wide or wider as the dorsal sinus (24:6) (very narrow, or occasionally even absent, in *Eutritomaria* (23:5-7)). Furthermore, the entire plant is decumbent in growth while *Eutritomaria* and *Saccobasis* are more ascending to erect, and tend much more to form caespitose tufts, rather than flat mats. The development of a decumbent mode of growth represents an innovation in the genus, and has probably occurred independently of *Dilophozia* (hence does not indicate any close relationship to *Dilophozia*).[30]

However, the less extremely asymmetrical lobes of the leaves suggest *T. scitula*, which may also be rather decumbent in growth. In the latter, furthermore, the leaf-insertion is often less transverse (22:4) and the leaves are scarcely more complicate-canaliculate (compare 22:7 with 23:6). This species possibly may serve as an indication of what the common ancestral form for

28 It must be stressed, however, that the degree of dorsiventral differentiation of the medulla is often relatively slight. Buch figures the ventral half of the medulla of *T. quinquedentata* as occupied by small, mycorrhizal cells. In 24:5 only the ventral fourth of the medulla is so differentiated. Similarly, in *Barbilophozia* there may be a slight differentiation of a ventral band (compare 7:1 and 8:6, in which there is supposedly no ventral band of smaller cells with 24:5, in which there is supposed to be such dorsiventral differentiation). Again, *Saccobasis*, with a dorsiventral differentiation of the medulla (25:8) really differs only in degree of development of such a ventral band from *A.* (*Eurylobus*) *saxicolus* (19:9), which is supposed to lack a ventral band. Buch (1933) I believe correctly stressed the relationship between these smaller ventral cells and mycorrhiza. In all of the groups with a "ventral band" (no matter how poorly developed it may be), the older portions of the stem becomes brownish and show distinct infestation with mycorrhiza in the small-celled medullary band. In the species without a ventral band mycorrhizal infestation is limited to the cortical layer of cells (compare 1:5 with 25:8); however, even in the species with a dorsiventral differentiation of the medulla there may be little or no mycorrhizal infestation in younger stems (compare 15:5, 15:7 and 17:8).

29 I am not too impressed by the difference in the stalk of the antheridium. I find that in *T. scitula*, for instance, the stalk is usually uniseriate, but may have occasional cells divided by a vertical wall (compare 22:5 and 6). I have also studied the antheridial stalk of *T. exsectiformis* and find it to vary exactly as in *T. exsecta*, i.e., some stalks are uniseriate throughout, while others have one or two of the cells divided by a vertical wall (thus resulting in a partly biseriate stalk). The variability in this regard is even more extreme in other Lophozioid species. In *L.* (*Leiocolea*) *gillmani*, for instance, I have found stalks uniseriate throughout, or biseriate throughout, or even triseriate at base and biseriate distally: all in antheridia from a single androecium.

30 In *T. scitula*, however, the plants are also nearly or quite decumbent in growth, except for the strongly dorsally curving apex of the plant.

T. quinquedentata and the *T. exsecta* complex must have looked like.

It is therefore obvious that *T. quinquedentata* has no close relatives among the genus. If we are to recognize such small groups as *Orthocaulis* and *Massula*, it becomes desirable to segregate *T. quinquedentata*, as done on page 65.

THE TRITOMARIA-SACCOBASIS PROBLEM

Meylan (1924) first separated *J. polita* from the other Lophozioid groups, but as the genus *Jungermania*—a procedure which has found no following, for nomenclatorial reasons. For the same taxonomic entity Buch (1933) selected the name *Saccobasis*. Meylan already called attention to the fact that the dorsal end of the leaf-insertion is directed towards the stem-apex, the reverse of what occurs in all the other Lophozioid genera (25:2,5). Buch used this, together with the extremely pachydermous nature of the cortical stem cells (and their unusually elongate form) (25.9) as the basis of his genus.[31] Admitting the unusual leaf-insertion as a taxonomically significant peculiarity, it must be stated that it can be derived from such a type as *T. exsecta* by the development of postical decurrence of the ventral lobe (and consequent basal curvature of the line of insertion), together with an apical curvature of the dorsal line of insertion. This results in an undulate line of insertion (25:3-4). There seems to be no reason for considering *Saccobasis* as other than a highly side-wise specialized species derived from a common ancestral form with *T. scitula* by: development of an undulate line of leaf insertion; gradually developing obsolescence of the leaf-sinuses, resulting in short, often obtuse lobes (25:6-7); development of more elongate and more pachydermous cortical cells (25:9); development of larger leaf-cells.

It should be noted that even in *Eutritomaria* the cortical dorsal cells of the stems are relatively elongate (compared with *Dilophozia* and other groups), and average between 2.5 and 3.5 or even 4.0 times as long as wide (compare 22:2,3 with 25:9,10); furthermore, their width is somewhat less than that of the basal leaf-cells. (In *T. scitula*, for instance, the cortical stem cells are 16-20 μ wide x 36-68 μ long, while the basal leaf-cells are 20-25 μ wide). It is therefore apparent that the extremely elongate dorsal cortical cells of *Saccobasis* are but an extreme development of a condition that also characterizes *Tritomaria*.[32]

---

31 It is obvious from 25:8-9 that the cell-walls of the cortical layer may be merely moderately thick. Frye and Clark's separation of *Saccobasis* because of supposedly extremely thick cortical cell-walls therefore lacks validity.

32 Furthermore, there is considerable intrageneric variation in the relative widths of the cortical stem and basal leaf-cells, and in the length of the cortical stem-cells. Buch (1933), Evans (1935) and Frye and Clark (1945) agree in that *Lophozia* (including *Massula*) has the cortical cells merely 1-2 times as long as wide, and slightly wider than the basal leaf-cells. However, even within one subgenus of *Lophozia* (*Massula*) there is an extraordinary amount of variation in this regard. *L.* (*Massula*) *obtusa*, for instance, has the cortical stem cells subequal in width to the basal leaf-cells, and 1.5-3 times as long as wide (compare 9:1 and 2). In *L.* (*Massula*) *marchica* the cortical stem cells are 4-8 times as long as wide and often almost exactly half as wide as the basal leaf-cells (compare 12:2 and 3). The difference in cortical stem-cells therefore cannot be considered to be of any great importance, and I would not regard the elongate cortical cells of *Saccobasis* as of generic importance, *per se*.

ANASTROPHYLLUM Spr. emend. Schuster

THE SPHENOLOBUS-ANASTROPHYLLUM PROBLEM

The genus *Anastrophyllum* has been one of the difficult complexes and its relationships have remained unsatisfactorily defined. Müller (1910:580), discussing *A. reichardti* (Gottsche) St., states that it shows the generic characters of *Anastrophyllum* (which he delimited very narrowly) "less clearly, and therefore one placed the plant in *Sphenolobus* previously. It admittedly shows relationships to some species of the last-named genus, and binds together to a certain degree both genera *Anastrophyllum* and *Sphenolobus*." Buch (1933) did not accept the circumscription of *Anastrophyllum* as attempted by Stephani (1893) or Müller (1910) (based essentially on the extremely secund leaves and broadly clasping leaf-bases), but placed also the species *Sphenolobus michauxii* in *Anastrophyllum*, because it had the leaves widest basally, with the dilated dorsal base extending across the stem, and decurrent on it. Buch overlooked the fact that *Sph. saxicolus* also has this type of leaf-insertion and a somewhat dorsally decurrent base (compare 19:1,4,5,6 and 21:17-20), even if somewhat less strongly developed. In the writer's opinion, there is therefore a virtual continuum: *Sph. saxicolus* → *A. michauxii* → *A. reichardti* → *Anastrophyllum* s. str. A generic break between any of these groups can scarcely be attempted. These groups further agree in the distinctly collenchymatous leaf-cells (gradually becoming more marked as one goes from *saxicolus* to *michauxii* to the more specialized species), which never occur in *Sph. minutus* (compare 19:2 and 21:10 with 20:8). They further agree in that the capsule-wall remains 3-4 or even 5 cell-layers thick. The writer therefore believes that this developmental line cannot be broken into generic groups (at best into subgeneric groups).

The fact that Müller (1910) admits the difficulty in separating *Anastrophyllum* from *Sphenolobus*, and that his separation did not follow along the lines suggested by Buch (1933), together with the fact that I cannot find either of these attempts at a separation satisfactory suggests that we are attempting a generic separation where one does not exist. Andrews (1948) has also recently suggested that if *A. michauxii* is placed in *Anastrophyllum*, there is no reason why *Sph. saxicolus* should not be placed in it.

It is therefore evident that no sharp break exists between *Sphenolobus saxicolus* and *Anastrophyllum* (sensu Buch, 1933, Müller 1939). The sharpest break, in my estimation was totally obscured when Buch placed *Sph. saxicolus* and *Sph. minutus* together into his genus *Sphenolobus*. Utilizing his narrow generic concepts, such a genus as *Sphenolobus* was entirely heterogeneous, in spite of the fact that it included only two species. This problem next needs elucidation.

THE SPHENOLOBUS MINUTUS-SPH. SAXICOLUS PROBLEM

The above two species differ in a number of fundamental features, as is evident from the key (p. 35) and as will emerge from the following discussion (see also the discussion under *Anastrophyllum*, s. lat.). The point I

should like to stress here is that the most fundamental break between the entire *Anastrophyllum-Sphenolobus-Crossocalyx-Eremonotus* complex occurs between the two species now cited under *Sphenolobus*. The entire classification of the complex, therefore, is extremely unsatisfactory. *Sph. saxicolus* agrees with *Anastrophyllum* (s. str., the subgenus *Euanastrophyllum* of the following treatment) in the basic type of leaf-insertion, collenchymatous leaf-cells, morphology of the capsule, relatively high stem, etc. *Sph. minutus* agrees with the *Crossocalyx-Eremonotus* complex in exactly those features that separate it from *Sph. saxicolus*, namely, the transverse, non-decurrent dorsal end of the leaf-insertion, with the basal part of the leaf not extending beyond the dorsal midline of the stem; in the very small, more or less equally thick-walled leaf-cells; in the reduction to a bistratose capsule-wall; in the reduced stem (10-11 cells high). These features are cited as relatively fundamental by Buch (1933) and Müller (1948). Therefore, if any generic division is attempted in the complex, it must be attempted along new lines.

In my estimation the relationship between *Sph. minutus* and *Sph. saxicolus* (though not close) is not distant enough to warrant separate genera. I therefore place these groups in discrete subgenera within the one large genus *Anastrophyllum*. If a division into two genera is held desirable it will, I believe, prove more natural across the lines indicated in my key (Couplet 12), rather than along the lines proposed by Buch (1933) and accepted by Müller (1948). Furthermore, the stem morphology does not support a division as indicated by Buch. The large *A. michauxii* and *saxicolus* have the stem about 14-16 cells high. The medium sized *A. minutus* about 10-11 cells high, the very small *A. hellerianus* and *myriocarpus* only 6-7 cells high. All of the forms have the medulla uniform, and free of mycorrhiza, with any mycorrhizal invasion limited nearly to the cortex.

The name *Anastrophyllum* should be used for such a large genus, rather than *Sphenolobus*, in spite of the fact that the latter was proposed in 1874, two years before the former. Lindberg used *Sphenolobus* first as a subgenus of *Jungermania*, while Spruce proposed *Anastrophyllum* as a subgenus of *Jungermania* (in 1876). However, the earliest use of either name as a generic name dates from 1893, when Stephani used *Anastrophyllum* as a genus in (Hedwigia, 32: 140), while *Sphenolobus* was not used as a genus until 1902, by Stephani (Bull. Herb. Boissier, Ser. 2, 2: 164, and Spec. Hep. 2: 156). Therefore, *Anastrophyllum* has priority as a generic name.

The writer would follow Meylan (1939) and Müller (1940, 1947) in using *Crossocalyx* for *A. hellerianus*, rather than *Isopaches* (which has theoretical priority). The first species mentioned by Buch (1933, p. 288) under *Isopaches* are *I. bicrenata* and *decolorans*, which are congeneric and in my estimate form a discrete subgenus of *Lophozia*. I would consider *I. bicrenata* as the type, which would therefore leave *I. hellerianus*, which is not congeneric with *I. bicrenata*, without a subgeneric name available except for Meylan's *Crossocalyx*.

The genus *Anastrophyllum*, as delimited here, is considered to include two

divergent series, one leading from the archetype to *Sphenolobus* (s. str.) → *Crossocalyx* → *Eremonotus*. The other developmental line leads from the relatively unspecialized *Eurylobus saxicolus* to *A. michauxii* to *Anastrophyllum* s. str. As is expressed above, the most fundamental break occurs between these two series, between "*Sph. minutus*" and "*Sph. saxicolus*." If a more "radical" generic grouping is desired the first three subgenera can be placed in a genus by themselves (for which the name *Sphenolobus* is available, as well as *Eremonotus*). The latter name, dating from 1900 (Pearson, Hep. of the Br. Isles, p. 200) precedes *Sphenolobus*, and should be used for the genus, as follows:

EREMONOTUS Lindb. & Kaal.

1. Subgenus *Sphenolobus* (Ldb.) St.
2. Subgenus *Crossocalyx* Meyl.
3. Subgenus *Eueremonotus* subg. n. (*E. myriocarpus*).

The second genus would include only two subgeneric groups, as follows:

ANASTROPHYLLUM (Spr.) St.

1. Subgenus *Eurylobus* subg. n. (*A. saxicolus*).
2. Subgenus *Euanastrophyllum* Schuster (1949).

Müller (1947, p. 43) already suggested that perhaps *Crossocalyx* and *Eremonotus* should not have been separated generically, but should have been retained as subgenera of *Sphenolobus* (a view which is expressed above). However, the oldest generic name of the three is *Eremonotus*, and I therefore cite that as the generic name. Müller stressed the fact that in both *Crossocalyx* and *Eremonotus* the perianth bears a deep dorsal furrow. This is decidedly also the case in *Sphenolobus minutus* (see 20:1), although slight supplementary lateral furrows occur (and these are also indicated in some perianths of *Eueremonotus* and *Crossocalyx*).[33] It would seem, therefore, that these three "genera" bear so many fundamental characteristics in common

33 The presence of a dorsal furrow of the perianth does not seem too fundamental to me in attempting a separation between the *Anastrophyllum* and *Sphenolobus-Crossocalyx* complex. It appears to recur again in at least some species of *Anastrophyllum* subg. *Euanastrophyllum*. Although the perianth is strongly inflated and clavate (secondarily) in *A. michauxii* there is still an indication of a dorsal furrow or groove (and such is indicated in the Fig. 292 b in K. Müller, 1910, p. 601). A similar dorsal groove also appears to occur at least occasionally in "*Sph.*" *saxicolus* (and again is indicated in Müller, 1910, p. 604, fig. 293b). In *A. reichardtii* Evans (1900, Pl. 16) also figures a deep dorsal groove, extending down towards the base. It therefore seems that throughout the genus *Anastrophyllum* (s. lat., as in this paper) there occurs at least a sharp tendency to produce a dorsal longitudinal groove of the perianth. This appears to be fundamentally distinct from *Tritomaria* (which was once placed in *Sphenolobus*), in which there is a distinct dorsal fold, usually extending to near the perianth base. See 23:5, and also K. Müller, 1910, Fig. 294a, p. 607, where such a dorsal fold is indicated for respectively *T. exsectiformis* and *T. exsecta*. Compare 23:5 with 20:1, where the differences in perianth form between *Anastrophyllum* and *Tritomaria* are correctly indicated.

that a separation into three monotypic generic groups is certainly not warranted (see p. 72).

Müller goes on to state that since these groups differ from *Sphenolobus* in the seta cross-section, he is willing to let them remain — a procedure which I cannot follow. On a previous page Müller (p. 40) had criticized Buch for attempting to separate genera because of slight differences in number of rows of cells in the axis of the gametophyte (i.e., stem), and states that "Die Zahl der Zellen des Stengelquerschnittes wird lediglich durch die Grösse der Pflanze bedingt." The number of rows of cells in the axis of the sporophyte (e.g. seta) is in my estimation similarly bound up with the total size of the plant, hence of no more real significance than the size of the stem. Buch (1942, p. 284) has also stressed this. Since the only real difference between *Sph. minutus* and *Crossocalyx+Eremonotus* lies in the seta section, I believe subgeneric separation to be more expressive of the actual relationship than generic segregation.

THE SPHENOLOBUS-CROSSOCALYX PROBLEM

The inclusion of *Sph. hellerianus* in *Isopaches*, by Buch (1933, 1942) completely obscured the real relationships of the species, in the writer's opinion. *Sph. hellerianus* agrees with *Sph. minutus* (and *Eremonotus*) in having a bistratose capsule-wall; a reduced stem 11 or fewer cells in height; complicate-canaliculate leaves, with the dorsal end of the insertion transverse; more or less equally thick-walled leaf-cells (see p. 26). In addition, the more or less distinct dorsal longitudinal fold of the perianth (becoming obscure as the capsule matures) (compare 20:1 with 21:8) is shared by these three groups. As previously stressed, therefore, I would more closely associate *Sphenolobus minutus* and the *Crossocalyx-Eremonotus* complex (which could conceivably be set off as a discrete genus, as is indicated previously).

The inclusion of *Sph. hellerianus* in *Isopaches* (followed by both Frye and Clark, 1945, and Evans, 1935) has been sufficiently criticized by Meylan (1939) and Müller (1947, 1948), and need not be treated further here. It is only necessary to compare the figures of *Sph. minutus* and *C. hellerianus* (Pl. 20 and 21) with those of *Isopaches* (Pl. 13) to see that the leaf-form and especially the type of shoot produced with gemmae-formation would ally *Sphenolobus* and *Crossocalyx*, but not *Crossocalyx* and *Isopaches*.

THE ANASTROPHYLLUM-ORTHOCAULIS PROBLEM

Not only is it difficult to find satisfactory lines along which to divide the genus *Anastrophyllum* (s. lat., as used on p. 35 into generic groups, but an objective student will admit that it is extremely difficult to find a sharp line of demarcation between *Orthocaulis* and *Anastrophyllum*.

The less derivative species of *Orthocaulis* (such as *kunzeanus*) differ at once from the entire *Anastrophyllum* complex in retaining a presumably atavistic tendency for the leaf-lobes to undergo secondary division (resulting in a 3, rarely 4-lobed leaf) (1:6; 2:1-2), and in the retention of broad ventral

stem-sectors able to produce underleaves (1:6). However, in the more specialized forms, the leaf-lobes may be almost constantly bilobed (as in 1:1), and the ventral stem-sectors may be reduced to a width of 2 cells and lack the ability to develop any trace of underleaves (2:2). We are further forced to concede that even in the *Anastrophyllum* complex the least specialized species may sometimes retain the ability to develop 3-lobed leaves (as in 19:1, upper leaf), with exactly identical division of the ventral lobe, as in *Orthocaulis*. A third difference cited by authors in separating *Anastrophyllum* (including *Sphenolobus*) from *Orthocaulis* is the leaf-insertion, which is supposedly transverse dorsally in the first, oblique and decurrent in the second group. In the large, less reduced forms of *Anastrophyllum* (such as *A. saxicolus*), the dorsal third of the line of insertion is equally oblique in many cases, and the line of insertion, in lateral view is nearly identical with that of some species of *Orthocaulis* (compare 19:1 with 1:1 and 2:1 and 3:10; compare 19:6 with 3:1). Furthermore, the stem-anatomy of the less reduced species is virtually identical in both groups (compare 19:9 with 1:5). Finally, the *Anastrophyllum-Sphenolobus* complex supposedly differs in the complicate-canaliculate leaves from *Orthocaulis*, in which the leaves may be somewhat concave, but not distinctly complicate. Unfortunately this distinction is also not absolute. Xeromorphic modifications of *L.* (*O.*) *kunzeana* (the "var. *plicata*") may have the leaves virtually complicate-canaliculate (compare 1:1 with 19:1 and 20:2) and *L.* (*O.*) *atlantica* often has the leaves strongly concave-complicate (3:10). Furthermore, *A. hellerianus* may have the leaves merely concave (note median leaves in 21:3).

It is therefore evident that it is extremely difficult to cut a sharp generic line between the more advanced species of *Orthocaulis* (such as *binsteadii* and *atlantica*), and the less derivative ones of *Anastrophyllum* (such as *saxicolus*). *Orthocaulis* very definitely shows an evolutionary tendency similar to that which the *Anastrophyllum* complex must have undergone. The retention of a generic distinction between *Orthocaulis* and *Anastrophyllum* thus may well be questioned by more conservative workers, and is maintained here largely because it seems better to separate the long developmental line *L.* (*O.*) *binsteadii* — *A. saxicolus* — *A.* (*S.*) *minutus* — *A.* (*C.*) *hellerianus* — *A.* (*E.*) *myriocarpus* into at least two main segments.[34]

---

34 The very close relationship between *Anastrophyllum saxicolus* and *Orthocaulis* is clearly indicated by the fact that Frye and Clark are reduced to using minor differences in pigmentation of the cell-walls and thickness of cell-walls and trigones in attempting to separate the three groups, as follows:

J. Walls of median leaf-cells thick or moderately so.
K. Trigones in leaf-middle yellowish, large to bulging .....*Anastrophyllum*
K. Trigones in leaf middle whitish, small to large but not bulging ....*Sphenolobus*
J. Walls of median leaf-cells thin or only slightly thickened .....*Orthocaulis*

As is evident from comparing 19:2 (*Sph. saxicolus*) with 2:8 and 3:2 (*Orthocaulis*) the separation J-J cannot be upheld, and there is *no difference* between *Sph. saxicolus* and *Orthocaulis* in this regard.

Synthesis of a New System of the Lophoziaceae

From the preceding detailed discussion has emerged the fact that a considerable number of features of previous classifications were open to criticism. It was concluded that:

1. *Lophozia* is best delimited broadly (as in Müller, 1939, Müller 1910, Meylan, 1924, Macvicar, 1926, Schuster, 1949, etc.) including essentially forms with obliquely inserted leaves (contrasted to *Anastrophyllum* and *Tritomaria*, in which they are essentially transversely inserted dorsally).
   - A. If the genus is at all to be subdivided, a division into three genera (*Barbilophophozia, Leiocolea, Lophozia* s. str.) may be attempted, the first two retaining underleaves, the latter lacking them. 35 No division into genera on the basis of stem-structure is warranted, at least not on the basis proposed by Buch (1933, 1942).
   - B. Such a division into three genera, though perhaps phyletically justified, is taxonomically difficult to carry through (because of secondary loss of underleaves in such species as *Leiocolea badensis, Barbilophozia barbata* and *attenuata*, etc.). Therefore, for practical reasons (and because there is no pressing phyletic reason indicating the opposite), these latter groups are retained within *Lophozia*, s. lat.
   - C. *Orthocaulis* can be, tentatively, retained as subgenerically distinct from *Barbilophozia*.36
2. *Tritomaria* is only doubtfully distinct from *Lophozia* s. lat., and if to be retained generically, should include the related element *T. quinquedentata* and perhaps *Saccobasis polita* as discrete subgenera.
3. *Anastrophyllum* should be defined more broadly, since *Sphenolobus* cannot be sharply separated from it. Similarly, *Crossocalyx* cannot be sharply separated from *Sphenolobus minutus*, and is best treated as a subgenus.
   - A. If any attempt is made to divide the elements I include in *Anastrophyllum* into "genera," this cannot be done on the basis employed by either Müller (1910, 1939-1940) or Buch (1933, 1942).
   - B. If such an attempt is made it probably should be made on the basis of the 2-stratose capsule wall of some groups (*Crossocalyx, Eremonotus, Sphenolobus minutus*) vs. the 3-5 stratose capsule-wall of the other groups (*Sph. saxicolus, Anastrophyllum* s. str.), and on the basis of other correlated differences.
4. *Temnoma* and *Gymnocolea* are unquestionably good genera, hence need not be further discussed in this connection, because of the universal concurrence of opinion here.

Allowing for subjective differences in interpretation of the rank to be accorded several of these categories, two systems can be set up which are essentially in accord:

"Conservative"	"Radical"
1. Lophozia	1. Barbilophozia
A. Subgenus Orthocaulis	A. Subgenus Orthocaulis
B. Subgenus Barbilophozia	B. Subgenus Eubarbilophozia
C. Subgenus Leiocolea	2. Leiocolea
	3. Lophozia
D. Subgenus Massula	A. Subgenus Massula
E. Subgenus Isopaches	B. Subgenus Isopaches
F. Subgenus Dilophozia	C. Subgenus Dilophozia

35 Why such a separation is difficult to maintain is discussed at length under *Lophozia* subgenus *Massula*.

36 See p. 19 and p. 41 in this regard.

2. Tritomaria	4. Tritomaria
A. Subgenus Eutritomaria	A. Subgenus Eutritomaria
B. Subgenus Trilophozia	B. Subgenus Trilophozia
3. Saccobasis	5. Saccobasis
4. Anastrophyllum	6. Anastrophyllum
A. Subgenus Eurylobus	A. Subgenus Eurylobus
B. Subgenus Euanstrophyllum	B. Subgenus Euanstrophyllum
	7. Eremonotus
C. Subgenus Sphenolobus	A. Subgenus Sphenolobus
D. Subgenus Crossocalyx	B. Subgenus Crossocalyx
E. Subgenus Eremonotus	C. Subgenus Eueremonotus
5. Temnoma	8. Temnoma
6. Anastrepta	9. Anastrepta
7. Gymnocolea	10. Gymnocolea
8. Mesoptychia	11. Mesoptychia
9. Acrobolbus	12. Acrobolbus

Since the last five genera (in both columns) would be equally acceptable to either conservative or more "radical" workers, they will be only briefly discussed in the following pages, and are illustrated only in part.

The genera (and included subgenera) are here arranged, as far as possible, in a sequence, starting with the least specialized and going to the most highly specialized. A linear arrangement, obviously cannot express true relations (for this see Tables I and II, in summary). The isolated genera *Temnoma* (closely related to *Orthocaulis*), *Anastrepta* (most closely related to *Lophozia*, s. lat.), and *Gymnocolea* (related very probably to *Lophozia* subgenus *Isopaches*) are *extremely* distantly related, and their juxtaposition cannot be taken to indicate any phyletic relationship. Similarly, the last two genera (*Acrobolbus* and *Mesoptychia*) represent the apices of long and independent evolutionary lines, and still have to be adequately studied to verify their position within the Lophoziaceae.

KEYS TO GENERA AND SUBGENERA OF LOPHOZIACEAE

Phylogenetic Key[37]

1. Perianth well developed and quite free from bracts, never forming a perigynium at base, lying in the axis of the stem (5:1; 6:6-7; 11:9; 17:1; 20:1) (leaves distinctly lobed, never with marginal rhizoids) ..... 2.

2. Leaves lobed 0.08-0.5 (occasionally to 0.6) their length into 2-4 lobes, the lobes not finger-like, not channeled and not with the margins reflexed (1:6; 2:5-6; 3:1; 5:6-7; 7:8; 9:1, etc.); perianth obtusely 4-5-plicate terminally (one or more plicate occasionally attaining the base of the perianth) or smooth (5:1; 6:6-7; 17:1; 20:1; 23:5); ventral stem-sectors 1-12 cells wide usually, the ventral merophytes occupying less than 0.25 the stem periphery (usually less than 0.15) (1:6; 6:8; 12:5; 18:2; 19:4; 20:3); leaves obliquely inserted: the ventral two-thirds of the line of insertion at an angle of 15-60° to stem ..... 3.

---

37 Since this key entails study of certain anatomical features (stem sections, etc.) and cytological characters (oil-bodies), as well as sporophytic characters, it may not always be usable for dead sterile material. The working key, p. 37, is therefore given, to supplement the present key.

3. Postical (ventral) leaf-margin broadly, strongly reflexed,[38] the dorsal slightly reflexed; posterior half of leaf nearly transversely inserted, dorsal half much more obliquely inserted, decurrent; leaves bilobed only 1/12 - 1/6 their length, the apical half more or less strongly dorsally convex; oil-bodies 2-4 μ, either homogeneous or consisting of 2-4 oil-globules ..... *Anastrepta* (Ldb. et Arn.) Schiffn.

3. Postical leaf-base never sharply reflexed (normally more or less flat or incurved) (1:1; 2:1; 8:1-3; 10:2; 19:1, 5, etc.); posterior half of leaf always obliquely inserted (usually more so than dorsal half) (8:1; 9:1; 10:6; 18:4; 20:3); leaves bilobed 0.15-0.6 their length, or 3-4-lobed, the leaves generally more or less adaxially concave; oil bodies various ..... 4.

4. Leaves with the line of insertion oblique throughout; the dorsal end of the insertion distinctly directed towards stem-base (the ventral half also oblique in insertion) (3:1; 5:1; 8:1-2; 10:2, 5; 12:6; etc.). (Often with ventral stem-sectors remaining 4-12 cells wide and able to develop underleaves; leaves 2-4-lobed: if more than 2-lobed never with dorsiventral differentiation of the stem-medulla; leaves never strongly canaliculate or complicate-canaliculate: the dorsal lobe never lying over the ventral, the lobes lying generally in the same plane (1:3; 2:1; 5:1; 6:8; 9:4; 12:5; 16:4; 18:1-2, etc.))[39] ..... 5.

5. Leaves generally with acute or subacute lobes[40] (1:6; 2:4-6; 5:6-7, etc.); leaf-cells rarely equally thick-walled and capsule-wall generally 3-5 stratose[41]; capsule-wall with inner layer with annular (6:1), rarely semi-annular thickenings (13:11); perianth plicate (if smooth, beaked at mouth), persistent (5:1; 6:6-7; 17:1); perichaetial bracts more or less larger than leaves, generally differing from leaves in shape (usually with more lobes and/or with marginal teeth) (13:2; 14:8; 17:6); rhizoids forming a dense ventral mat; gemmae generally common; stem 8-22 cells high[42] (1:5; 5:8; 7:1; 8:6,11; 10:9; 13:8; 14:7) ..... *Lophozia* Dumort. s. lat.

6. Leaves 3-4-lobed (at least on well-developed shoots), often with postical bases with 1-several cilia (1:6; 2:1-2, 4-6; 3:1; 7:2, 8; 8:1-3) ventral stem-sectors well-developed, 4-12 cells wide, usually able to produce distinct underleaves[43] (1:6; 7:3-4; 8:3); perianth remaining plicate: medulla of stem uniform, lacking a small-celled mycorrhizal ventral band (1:5; 7:1; 8:6,11); capsule-wall 3-4-stratose, the inner layer with annular thickenings ..... 7.

7. Leaves generally 3-lobed, with dorsal lobe largest (1:6; 2:5-6; 3:1-11) (occasionally 2-lobed, in *O. quadrilobus* mostly 4-lobed); plants erect or strongly ascending in growth, with the leaves in-

---

38 Frye and Clark (1944, p. 337) in their key erroneously state "dorsal margin," but in the text (p. 398) correctly give the "ventral margin" as strongly reflexed.

39 In a few species of *Orthocaulis* (*L. binsteadii, kunzeana,* etc.) the leaves may be quite strongly concave and more or less complicate (see 1:1, 3:10). These species differ from all those falling under the second 4 (p. 34) in having some or many leaves 3-lobed, with the *dorsal* lobe the largest.

40 Only in *L. obtusa* are the lobes generally rounded at apex; this species, however, has the leaves generally much wider than long.

41 In *Isopaches,* however, the cells are equally thick-walled and the capsule-wall is bistratose.

42 In *Isopaches* only 8-10 cells high; in other groups usually 10-22 cells high.

43 In a few species of *Orthocaulis* reduced to width of 2 cells and unable to develop underleaves (see 2:2).

serted by an arched line of insertion (2:2; 3:1), the line of insertion at about 45°-60° angle, curving towards stem-apex; postical leaf-base with cilia of isodiametric cells, when present (1:4); cortical stem-cells often very thick-walled (1:5); leaves somewhat concave and with incurved lobes, occasionally canaliculate (1:1, 3; 2:1; 3:10) ..... Subgenus *Orthocaulis* Buch.

7. Leaves generally all or mostly 4-lobed (7:2,8; 8:1-3,5); plants horizontal in growth. with the leaves inserted by a nearly straight line of insertion at about a 25-30° angle (8:1,5,9); postical leaf-base with cilia, when present, of elongate cells (7:8); cortical stem-cells little or not thickened (7:1; 8:6); leaves nearly flat or somewhat dorsally convex, widely spreading, the lobes rarely distinctly incurved, the leaves never canaliculate (7:2; 8:1-3,5) ..... Subgenus *Barbilophozia* Lske. emd. Buch.

6. Leaves normally 2-lobed (occasional leaves 3-lobed), the postical bases lacking cilia[44] (5:6-7; 6:8; 9:4; 10:2; 15:9; 16:4); ventral stem-sectors usually unable to produce underleaves (or perianth smooth and beaked) ..... 8.

8. Perianth smooth, terete, at the mouth suddenly contracted into a short beak (5:1; 6:6-7); oil-bodies very large, 4-7 x 8-15 μ, mostly 2-5 per cell (5:3; 6:4-5); cuticle usually very distinctly papillose (5:3, cell to the right); ventral stem-sectors well-preserved, 4-more cells wide, usually developing distinct underleaves (6:8); medulla of stem unmodified (5:8); capsule-wall 3-4-stratose; antheridial stalk usually biseriate; cells of leaves usually very large (35-50 μ), and generally strongly collenchymatous (5:4; 6:5) ..... Subgenus *Leiocolea* K. Müller.

8. Perianth distinctly plicate, gradually narrowed towards apex, never beaked (11:9; 17:1); oil-bodies smaller, 2-4 x 3-8μ or less in size, mostly 8-50 per cell (10:7-8; 11:8; 12:7; 13:3; 14:2; 16:3,-5,8; 17:4); cuticle smooth or very finely papillose (11:4; 15:2); ventral stem sectors only 1-3 cells wide (or cells non-collenchymatous and oil-bodies 20-60 per cell) ..... 9.

9. Stem with medulla homogeneous: not dorsiventrally differentiated, free of mycorrhiza (9:8; 10:9) or the ventral 1-3 layers of stem-cells infested (13:8), the ventral medullary cells never distinctly smaller than the dorsal medullary cells; leaf-cells non-collenchymatous: either thin-walled (9:2; 11:1-2,8; 12:2) or equally thick-walled (13:3-4); leaves as wide or wider than long; male and female bracts generally more or less strongly dentate (13:2) ..... 10.

10. Cells thin-walled, relatively large and usually 30-60 μ, with numerous (25-60) minute (2-4 μ) highly refractive oil-bodies per cell, whose contents are homogeneous or nearly (10:7-8; 11:8; 12:7); stems about 12 cells high, with cortical cells unable to produce thickened walls (9:1; 12:3), the cortical cells very similar to the interior cells (9:8; 10:9; 11:5; 12:1); mycorrhiza usually absent, or confined to the ventral cortical cells (12:1); ventral stem-sectors very wide (usually 10-12 cells or more), occasionally able to produce underleaves (9:4-5; 12:5); leaves very obliquely, nearly horizontally inserted, at an angle of about 15-35° (9:5; 10:6; 12:6); leaves generally distinctly wider than long (9:1,4,6-7; 10:2-5,11; 12:5), very often developing supplementary lobes or marginal teeth; capsule-wall 3-5-stratose, the inner layers

44 In *L. rutheana* occasionally with a single basal cilium.

thinner, with annular thickenings, the outer thicker, with nodular thickenings .....
.....Subgenus *Massula* K. M. emend. R. M. S.

10. Cells strongly thick-walled and small, 20-30 μ, with few (6-15) relatively large (4-9 μ), less refractive oil-bodies per cell, which are composed of numerous more or less distinct globules (13:3-4), the marginal cells usually lacking oil-bodies (13:4); stems merely 7-10 cells high, with the cortical cells becoming more or less strongly thick-walled (13:8); mycorrhiza usually present in the 1-3 ventral stem-layers (13:8); ventral stem-sectors very narrow (usually 2-4 cells wide at most), not able to produce underleaves; leaves inserted at an oblique angle of about 45-50° (13:7); leaves subcircular, no wider than long (13:7), never developing supplementary lobes or teeth (except when gemmiparous, as in 13:1); capsule-wall bistratose, both inner and outer layers with semi-annular thickenings (13:10-11), the two layers subequal in thickness .....Subgenus *Isopaches* Buch emend. K. M.

9. Stem with medulla distinctly dorsiventrally differentiated into a dorsal band of large, hyaline cells and ventral region of smaller and much shorter cells more or less destroyed by mycorrhizal activity (14:7; 15:7; 17:8), at maturity 10-22 cells high or more; leaf-cells generally collenchymatous (15:3; 16:3,5,8; 17:4), rarely scarcely so (14:2) never with equally thickened walls; leaves longer than wide (15:9; 16:2,6-7) or as wide as long (14:3; 17:5); male and female bracts with lobes not denticulate (17:1,6) except in *L. excisa* (14:8-9); oil-bodies generally 8-20 per cell, 4 to 4x8 μ, composed of distinct spherules (14:2; 16:3,5,8; 17:4); ventral stem-sectors obsolete, usually 1-3 cells wide (15:6; 18:2); capsule-wall 3-5-stratose, the inner layer with annular, the outer with nodular thickenings (as in 23:1-2) .....Subgenus *Dilophozia* K. M. emend. R. M. S.

5. Leaves with obtuse to rounded lobes (26:1,3,5-6,8); leaf-cells non-collenchymatous, becoming equally thick-walled and brownish; capsule-wall 2-stratose, both walls with nodular thickenings; perianth smooth, inflated, not beaked at mouth, caducous (26:1); perichaetial bracts identical in size and form with normal leaves (26:1); rhizoids very few and scattered (26:3,8); gemmae rarely developed; stem only 6-7 cells (26:2), with an undifferentiated medulla free of mycorrhiza; ventral stem-sectors narrow, only 1-3 cells wide (26:3,5), usually lacking underleaves or with very minute ones (26:4) on fertile shoots .....
.....*Gymnocolea* Dumort.

4. Leaves with the line of insertion oblique ventrally (19:4; 20:3; 21:6,17; 24:1-2; 25:1), but transverse dorsally, or directed towards the stem-apex (20:1-2; 21:7; 22:7-8; 23:5-6; 24:7; 25:2,5)[45]; ventral stem-sectors

---

45 This does not strictly hold for the species of *Eurylobus* and *Euanastrophyllum*: in these the dorsal half of the line of insertion may show an approach to the transverse condition, but the innermost edge of the line of insertion is distinctly decurrent along the dorsal midline (i.e., along the inner edges of the lateral merophytes of the stem) (see 19:1, 5-6; 21:18-20). These species, however, differ from all groups under the first 4 (p. 32) in that the leaves are strongly concave and either more or less canaliculate or cupped, with the lobes often incurved; they differ further from the obliquely-leaved groups in that the dorsal base of the leaf extends far across the stem-midline (compare 19:5 and 20:18 with 10.2, 18:1, etc.). The leaf in the latter groups is oblique throughout and not distinctly decurrent along the midline where the lateral merophytes meet: a condition fundamentally unlike that in *Eurylobus* and *Euanastrophyllum* (which however is scarcely evident from examination of lateral views of the stem).

obsolete, merely 1-2 cells wide (19:4; 20:3; 21:6,17; 24:2; 25:1), and unable to develop underleaves on vegetative shoots; leaves 2-lobed (and medulla uniform) or 3-lobed (and medulla dorsiventrally differentiated); leaves generally more or less concave-canaliculate to complicate-canaliculate (19:1,5; 20:1-2,7; 21:7,18,20; 22:7-8; 23:5-6; 24:7; 25:1-5), the dorsal lobe lying over the ventral on most well-developed sterile leaves.. .....11.

11. Leaves uniformly bilobed, with the dorsal lobe somewhat smaller than the ventral (19:1,3-7; 20:1-4; 21:3,6-7,17-20); stem with medulla homogeneous, lacking mycorrhiza or with them confined to the peripheral 1-3 stem-layers (19:9; 20:10; 21:2); plants erect or suberect in growth, with rhizoids sparse or none (19:6-7; 20:3,6; 21:3,17,19); leaf-cells merely 10-16 μ wide in leaf-middle; capsule-wall 2-4-stratose; cortical stem-cells relatively short and mostly 1-2.5 as long as wide 20:9), slightly wider than basal leaf-cells (compare 20:8 and 9); basal leaf cells 1-1.5 as long as wide. *Anastrophyllum* (Spr.) Steph., s. lat. .....12.

12. Capsule-wall 2-stratose; cells of leaf-middle more or less equally thick-walled and able to produce merely minute trigones (20:8; 21:1); normally developed leaves with dorsal half of insertion strictly transverse and not decurrent (20:1-2; 21:7); leaves not widest towards base, not expanded basally; the dorsal base of the leaf not expanded, extending merely to midline of stem (20:7; 21:3,7); plants able to develop gemmae on suberect or erect specialized shoots with erect to appressed, more or less sheathing, reduced leaves (20:6; 21:3); small species, with stem merely 5-10 (11) cells high in section (20:10; 21:2); antheridial stalk of a single row of cells; perianth scarcely to distinctly flattened above, oval in section, with a deep dorsal groove (at least when immature) (20:1; 21:8) .....13.

13. Seta in section of many rows of cells; stem 10-11 cells high in section (20:10); gemmae largely 2-4-celled (20:5); female bracts with entire lobes; leaves below inflorescences never with a basal tooth or lobe (20:1) .....Subgenus *Sphenolobus* (Ldb.) emend. R.M.S.

13. Seta in section merely of 8 peripheral and 4 inner rows of cells; stem only 6-7 cells high (21:2); gemmae largely or entirely 1-celled (21:4); female bracts with more or less dentate lobes; leaves below inflorescences generally with a basal tooth or lobe (21:7) .....Subgenus *Crossocalyx* Meyl.

12. Capsule-wall 3-4-stratose; cells of leaf thin-walled, but with small (19:2) to large and bulging (21:10) trigones; leaves with dorsal part of insertion not transverse, or only shortly so, the innermost edge distinctly decurrent on stem along dorsal midline (19:1,5-6; 21:18-20); leaves widest near or towards base, the dorsal base of leaf expanded, extending beyond midline of stem (19:1,5; 21:18,-20); plants with gemmae (when developed) on normal shoots with normally developed, widely spreading leaves; leaves with ventral (and sometimes dorsal) lobes often more or less incurved at apex (19:1,5; 21:18-20); larger species, with stems 12-16 cells high or more in section (19:9); antheridial stalk biseriate; perianth terete, strongly inflated distally, pluriplicate and often lacking a discrete dorsal longitudinal groove (19:8); seta in section of many rows of cells .....14.

14. Leaves much broader than long, cupped and hand-like (19:1,5), (19:3,8); leaf-cells unable to produce large trigones (19:2); female bracts erect, sheathing perianth, the lobes more or less

divided and dentate (19:7); dorsal leaf-lobes more or less incurved (19:1,5,7) .....Subg. *Eurylobus* subg. n.

14. Leaves as long or (usually) distinctly longer than wide (21:13), not strongly cupped, but usually strongly canaliculate, widest at base (21:13); leaf-cells able to develop large, bulging, yellowish trigones (21:10); female bracts usually spreading away from perianth, the lobes not subdivided, often entire; dorsal leaf-lobes spreading or squarrose (in our species), or lying loosely over ventral (21:18,20) .....Subg. *Euanastrophyllum* Schuster.

11. Leaves all or mostly 3-lobed (except on gemmiparous leaves) (22:7-8,10; 23:5-7; 24:1-2,6-7; 25:1-7); stem with medulla more or less dorsiventrally differentiated, the ventral 4-5 or more layers of medullary cells much smaller, becoming mycorrhizal and brownish (22:1; 24:5; 25:8), but the cortical cells free or nearly free of mycorrhiza; plants decumbent in growth (exc. *Saccobasis*) and with rhizoids numerous, usually forming a dense ventral mat (24:1), rarely sparse (25:4); capsule-wall 3-5-stratose; cortical stem cells somewhat to strongly elongate (22:2; 25:9), mostly 2.5-8 times as long as wide, averaging narrower than basal leaf cells; basal leaf-cells 1.5-4 as long as wide, and usually even most median leaf-cells very obviously elongate .....15.

15. Leaves with dorsal end of line of insertion transverse (22:7-8; 23:5; 24:7); ventral end of line of insertion oblique to transverse (22:4; 24:1-2), but never decurrent; dorsal end of line of insertion nearest stem-base (22:4; 24:1); leaves more or less strongly asymmetric (23:5-7; 24:1-2,6-7), rarely nearly symmetric (22:10), with acute or apiculate lobes; plants with strong ascending curvature of the shoot-apex; rhizoids forming a very dense ventral mat (24:1); stem with cortical cells mostly 2-3 times as long as wide (22:2); leaves in middle with cells 8-25 μ wide (average) .....16 . . . *Tritomaria* Schiffn. emend. Meylan.

16. Capsule-wall 3-stratose; antheridial stalk 1-seriate throughout or largely (22:5-6); leaves longer than wide, with narrow, acute lobes (22:10,12; 23:7), very distinctly canaliculate or complicate-canaliculate (22:7-8; 23:5-6); primary sinus separating the dorsal and median lobes deeper and wider usually than the secondary sinus between median and ventral lobes (22:7,8,10; 23:5-7); cells in leaf-middle 8-20 μ wide .....Subgenus *Eutritomaria* Schuster.

16. Capsule-wall 5-stratose; antheridial stalk biseriate; leaves as wide or wider than long, with broad lobes (24:2,6-7), little or not canaliculate (24:2,7); primary sinus between dorsal and median lobes not as broad as the secondary sinus between median and ventral lobes (24:2,6,7); cells in leaf-middle 22-25 μ wide .....Subgenus *Trilophozia* subg. n.

15. Leaves with dorsal portion of line of insertion directed obliquely towards stem apex (except for the slightly decurrent innermost edge) (25:2-5); ventral line obliquely directly towards stem apex (and with dorsal line forming a loop or basal pocket), but suddenly becoming strongly decurrent (25:1,3-4), the entire line of insertion thus strongly undulate; leaves symmetric, shallowly trilobed at the truncate apex (25:6-7), with obtuse lobes; plants nearly erect in growth and with shoot apex virtually lacking any autonomous dorsal curvature; rhizoids scattered, long, rather sparse (25:4); stem with cortical cells mostly 4-8 times as long as wide (25:9), much longer than basal leaf-cells (25:10); cells of leaf-middle 25-32 μ wide .....*Saccobasis* Buch.

2. Leaves lobed 0.7-0.9 their length into 4 (on some leaves 3) lobes, the lobes narrow, finger-like, channeled and with reflexed margins and sinuses (4:6-10); perianth deeply, sharply 7-9 plicate to near base; ventral stem sectors 10-16 cells wide or more, the ventral merophytes occupying 0.25 the stem-periphery (4:8); leaf-insertion subtransverse (at about a 70-80° angle with stem) (4:7,10) ..... *Temnoma* Mitt.

1. Perigynium present, terminal, at right angles to the stem ..... 16.

16. Perianth present, about as high as perigynium (28:6); calyptra free from perigynium (28:6); stems over 12 cells thick (27:11); leaves strongly asymmetrical, bilobed less than 0.2 their length, wider than long, their margins never rhizoidous (27:1,5-6); large underleaves on sterile shoots, bilobed and ciliate, the ventral stem-sectors circa 8-12 cells wide (27:7-8; 28:1-2,4) ..... *Mesoptychia* (Ldb.) Evs.

16. Perianth absent, the densely rhizoidous perigynium not capped by a perianth; calyptra "adnate to perigynium-wall"; stems merely 6-8 cells high (at least in American species); leaves bilobed deeply, for more than 0.25 their length, more or less symmetrical, not wider than long; leaves rhizoidous (in American species); underleaves absent or rare and vestigial on sterile shoots, the width of the ventral stem sectors negligible ..... *Acrobolbus* G. L. & N.

Artificial (Working) Key to Genera and Subgenera

1. Leaves 2-4-lobed for 1/6-4/5 their length (1:6; 2:5-6; 4:6; 19:3); leaf-margins never strongly reflexed, the leaves concave or flat (1:1; 3:1; 7:2), rarely slightly convex (5:1) ..... 2.

1. Leaves subentire, divided by an obscure, shallow sinus for about 1/10-1/12 their length into two broad lobes; leaf-margins more or less reflexed, the adaxial leaf-surface convex ..... 20.

2. Leaves unable to produce marginal rhizoids (1:6; 2:5-6; 19:3, etc.); a perianth present but no perigynium (5:1; 20:1) ..... 3.

2. Leaves able to produce marginal rhizoids; no perianth but a distinct rhizoidous perigynium at right angles to the axis; stem only 6-7 cells in height ..... *Acrobolbus*.

3. Ventral stem-sectors (merophytes) broad, at least 4-8 cells, often 10-16 cells wide (1:6; 4:9; 8:3; 9:4; 12:5); usually able to develop distinct underleaves; leaves often in part or entirely 3-4-lobed (1:6; 4:7; 8:1-3); stem with medulla uniform, lacking a small-celled ventral band (1:5; 7:3; 5:8; 10:9) ..... 4.

3. Ventral stem-sectors narrow, generally 1-2 (rarely 3-4) cells wide, the postical leaf-bases thus approaching the imaginary postical midline of the stem (2:2; 15:6; 18:2; 19:4, etc.); ventral stem-sectors never able to produce underleaves; leaves at most 3-lobed ..... 8.

4. Leaves all or largely 2-lobed (5:1,7; 6:8; 9:4), occasional ones irregularly lobed or with dentate margins (10:3,11; 12:5); leaf-insertion strongly oblique, the leaves horizontally spreading (5:1, 6:8; 9:1,4; 10:2,6; 12:5-6); oil-bodies specialized: either minute and homogeneous (11:8; 12:7), and 25-60 per cell, or very large and only 2-6 per cell (5:3; 6:4-5); leaf-cells generally large and 25-50 μ in leaf-lobes ..... 5.

4. Leaves all or mostly 3-4-lobed (1:6; 4:7; 8:1-3) (only *kunzeana* largely 2-lobed; if 2-lobed then concave and with erect or incurved lobes); if leaves nearly horizontally inserted, almost uniformly 4-lobed (7:2,8; 8:1-3); oil bodies of generalized type: moderate in sixe (4 x 8 μ), of numerous minute spherules, 4-20 per cell (2:7); usually with large, bifid or ciliate underleaves (1:6-7,10; 4:1-5; 7:3-4; 8:4,8); cells in leaf-lobes mostly 13-24 μ, with small to bulging trigones 6

5. Cells of leaves more or less collenchymatous, with distinct trigones and with a

papillose cuticle (except *L. badensis*) (6:4-5; 5:2-3); oil-bodies large, papillose, 5 x 10 μ or larger, mostly 2-5 per cell; perianth beaked (5:1; 6:6-7); cortical stem-cells generally somewhat thick-walled (5:8), the stems little flattened; leaves uniformly 2-lobed (5:6-7; 6:8) ..... *Lophozia* subg. *Leiocolea*.

5. Cells of leaves extremely thin-walled, lacking discrete trigones and with the cuticle normally quite smooth (9:2; 11:1-2,8; 12:2,7); oil-bodies minute, homogeneous, highly refractive, 2-4 μ usually, generally 30-60 per cell (10:7-8; 11:8; 12:7); underleaves normally absent (occasional in *L. obtusa*); perianth plicate, not beaked (11:9); cortical stem cells thin-walled like medullary (9:8; 10:9; 12:1); many leaves 3-4-lobed in some species or with scattered marginal teeth (10:3,11; 11:10; 12:4-5) ..... *Lophozia* subg. *Massula*.

6. Leaves nearly horizontal, inserted at an angle of 15-30°, spreading widely, flat or slightly dorsally convex, 4-lobed ¼-½ their length (7:2,8; 8:1-3,10); postical leaf-bases with cilia (when present) of elongate cells (7:8) ..... *Lophozia* subg. *Barbilophozia*.

6. Leaves concave, with erect or incurved lobes, not spreading, inserted at an angle of 50-80°, 3-4-lobed or partly 2-lobed (2:1; 3:1; 4:6-10); postical leaf-bases with cilia or teeth (when present) of isodiametric cells (1:4) ..... 7.

7. Leaves divided 1/4-2/3, the lobes with the margins not reflexed, not channeled (1:1,3,6; 3:1,3-8); leaves largely 3-lobed (except *L. quadrilobus*) ..... *Lophozia* subg. *Orthocaulis*.

7. Leaves divided 4/5 into 4 (rarely 3) lobes, the lobes narrow, with reflexed margins and sinuses, the lobes thus channeled and adaxially convex (4:6-10) ..... *Temnoma*.

8. Leaves all 2-lobed (only very occasional ones with ventral lobe divided, thus with a larger dorsal lobe) (1:1; 5:6-7; 6:8; 9:16; 20:1-4) ..... 9.

8. Leaves all or mostly 3-lobed, concave and more or less canaliculate or even complicate-concave (22:7,10; 23:5-6; 24:1-2; 25:1-7) ..... 17.

9. Plants with dorsal end of insertion quite oblique (3:1,10; 18:4) ..... 10.

9. Plants with dorsal half of insertion quite transverse (20:2,7;21:7); perianths with a deep dorsal groove, often extending down to near base on immature perianths (20:1; 21:8); leaf-cells very small (10-15 μ wide), equally thick-walled; gemmae on erect, filiform shoots with reduced leaves (20:6; 21:3); stem only 6-11 cells high (20:10; 21:2) ..... 16.

10. Ventral leaf-margins strongly reflexed; leaves bilobed merely 1/10-1/6 ..... *Anastrepta*.

10. Ventral leaf-margins flat or nearly, never reflexed (26:5-8; 17:2; 18:1); leaves bilobed 1/6-1/2 (3:1; 26:5-8) ..... 11.

11. Leaf-cells equally thick-walled, sometimes appearing guttulate (13:3-4); stems merely 6-8 cells high, with medulla never dorsiventrally differentiated (13:8; 26:2); leaves often circular, often as wide as long (26:5-8; 13:7) ..... 12.

11. Leaf-cells with thin-walls but more or less distinct trigones (3:2; 14:2; 15:3; 21:10); stems 9-22 cells high (14:7; 15:7; 17:8; 19:9) ..... 13.

12. Leaf-lobes rounded (26:1,5-8); gemmae usually absent, but generally with caducous perianths (26:1); rhizoids very few ..... *Gymnocolea*.

12. Leaf-lobes acute; gemmae usually present, perianths not caducous, plicate; rhizoids numerous ..... *Lophozia* subg. *Isopaches*.

13. Leaves strongly concave or concave-canaliculate, with at least the ventral lobe more or less incurved (19:1,5,8; 21:18,20; 1:1; 3:1), stems with medulla uniform, free of mycorrhiza and lacking a distinct ventral band of small cells (1:5; 19:9); plants erect or suberect in growth ..... 14.

13. Leaves spreading, little concave and canaliculate, with the lobes more or less spreading (and the entire distal half of the leaf in the same plane) (15:1;

16:4; 18:1); stems with medulla dorsiventrally differentiated, with a ventral region of smaller cells infested by mycorrhiza (14:7; 17:8) plants decumbent in growth usually ..... *Lophozia* subg. *Dilophozia*.

14. Leaves with dorsal bases not extending across the dorsal stem midline (3:10; 1:1; 2:1); occasional leaves 3-lobed; line of insertion of leaves somewhat convex towards stem-apex (2:4; 3:1) ..... *Lophozia* subg. *Orthocaulis*.

14. Leaves with dorsal bases expanded, extending most of the way across the stem 19:1,5,7; 21:18,20); leaves almost uniformly 2-lobed; line of insertion oblique nearly throughout, not distinctly curved towards stem-apex (19:6; 21:19) ..... 15.

15. Leaves much wider than long (19:3); leaf-cells little collenchymatous, with small trigones (19:2) ..... *Anastrophyllum* subg. *Eurylobus*.

15. Leaves as long or longer than wide (21:13); leaf-cells strongly collenchymatous, with bulging trigones (21:10). ..... *Anastrophyllum* subg. *Euanastrophyllum*.

16. Plants minute, 4-8 mm high (21:3); stems only 6-7 cells high (21:2); gemmae 1-celled, about 10 x 10 μ (21:4) ..... *Anastrophyllum* subg. *Crossocalyx*.

16. Plants larger, 1-3 cm long (20:1,6,7); stems 10-11 cells high (20:10); gemmae largely 2-4-celled, 10-15 x 15-30 μ or larger (20:5) ..... *Anastrophyllum* subg. *Sphenolobus*.

17. Dorsal cortical stem-cells 4-8 times as long as wide (25:9); dorsal half of leaf with line of insertion running up towards stem-apex (25:2-5); leaves equally 3-lobed for 1/10-1/6 their length (25:6-7) ..... *Saccobasis*.

17. Dorsal cortical stem-cells 1.5-3 times as long as wide (22:2); dorsal half of line of insertion of leaves transverse or decurrent towards stem-base (22:7; 3:10); leaves mostly decidedly unequally 3-lobed for ¼-½ their length (3:3-8; 23:6; 24:6) ..... 18.

18. Leaves when 3-lobed with dorsal lobe the shortest and smallest (23:5-6; 24:2,5-6); stem with a distinct ventral medullary region of small, brownish cells (22:1; 24:5); rhizoids forming a very dense ventral mat (24:1); dorsal end of leaf-insertion transverse (22:7-8) ..... 19.

18. Leaves where 3-lobed with dorsal lobe obviously the largest and longest (2:5-6; 3:3-8); stem with medulla homogeneous, free of mycorrhiza, and not distinctly dorsiventrally differentiated (1:5); rhizoids usually relatively sparse (3:1); dorsal portion of line of insertion obviously oblique (3:1,10) ..... *Lophozia* subg. *Orthocaulis*.

19. Leaves slightly to distinctly longer than wide, strongly canaliculate, the dorsal lobe separated from middle one by a sinus much wider than sinus separating middle lobe from ventral lobe (22:7-8,10; 23:5-7); leaf-cells 8-18 (20) μ wide in leaf-middle; gemmae abundant (22:7; 23:6) ..... *Tritomaria* subg. *Eutritomaria*.

19. Leaves as wide or wider than long, little canaliculate, more or less spreading on lax shoots, the dorsal lobe separated by a narrower sinus from middle lobe, than the middle lobe from the ventral lobe (24:1-2,6-7); median leaf-cells 20-25 μ wide; gemmae usually absent ..... *Tritomaria* subg. *Trilophozia*.

20. Underleaves common, bifid; a distinct perigynium present; leaves never transverse; no gemmae ..... *Mesoptychia*.

20. Underleaves absent or rare on sterile shoots; no perigynium; leaves with dorsal half very distinctly succubously oblique; gemmae common ..... *Anastrepta*

TREATMENT OF INDIVIDUAL GROUPS

LOPHOZIA Dumort., emend. K. Müller (1910)
(Plates 1-3, 5-18)

The genus Lophozia (which I circumscribe much as Müller did in 1910 and 1939), is perhaps the most difficult of the Nearctic generic entities to circumscribe. It is therefore unfortunate that the effort by Buch (1933) to

divide it into several more sharply circumscribable groups cannot be followed. The genus may be defined as follows:

Gametophyte with leaves 2-4 lobed (if 3-lobed, dorsal lobe obviously larger), inserted obliquely ventrally and obliquely to almost transversely dorsally, the leaf-plane either nearly vertical to the stem-axis (15:1, etc.) (*O. quadrilobus*) or nearly horizontal (5:1; 8-2) (*Barbilophozia*), but never with the dorsal half of the leaf folded over the ventral half (the leaf never distinctly concave-canaliculate, therefore).[46] Stem growing either suberect to decumbent; ventral stem sectors primitively about $^1/_5$ the width of the circumference (1:6), but often reduced to 1-2 cells wide (18:2), the underleaves from large and ciliate (5:4; 7:3-4) to absent (18:2). Perichaetial bracts usually larger than leaves and sheathing the perianth at base (17:1). Perianth never caducous. Capsule generally 3-5 stratose and with inner layer with annular (tangential and radial) bands (6:1) or with them semiannular (13:11).

It is evident that the diagnosis is in large part a negative one, serving to separate it from the less synthetic related genera *Tritomaria, Saccobasis, Anastrophyllum, Temnoma,* and *Gymnocolea*. This is due to the very variable types found in the genus. It is obvious from the diagram (p. 83) that *Lophozia* occupies a central position, from which there has been divergent evolution in numerous directions. These evolutionary "lanes" lead to groups very different in facies, and there has been, therefore, an attempt made to cut off these "lanes." Buch attempted a separation of generic nature along the line a-a, on the basis of stem structure. He considered this separation of fundamental value. As will be shown below, groups with identical stem-structure occur on both sides of this line, indicating there is no fundamental break at this point. Proof of the absence of such a fundamental break has led to the present attempt at a reclassification.

As is obvious from the outline (p. 30), *Lophozia* can be either broadly restricted (as here) or divided into three phyletically important elements that are rather distinct (*Barbilophozia, Leiocolea, Lophozia*). I here consider these as well-defined subgeneric elements. They can be separated by the key (p. 32), and may be briefly diagnosed as follows:

Subgenus 1. ORTHOCAULIS Buch

Large plants agreeing in all essential regards with *Barbilophozia,* except as follows: Plants growing suberect or strongly ascending (1:3), often with the rhizoids more sparse (3:1). Leaves variable, 2-4 lobed in different species, obliquely to subtransversely (*O. quadrilobus*) inserted, the insertion more or less arched towards stem-apex (2:4; 3:1; 8:9), ventrally usually slightly decurrent, basically 3-lobed on mature shoots (the ventral lobes then smallest, the dorsal larger, undivided except in *O. quadrilobus*), rarely horizontally spreading (8:10), but more or less concave and "cupped," often nearly hand-

[46] One or two species of *Orthocaulis* occur as xeromorphic modifications with more or less complicate leaves, such as *kunzeana* mod. *plicata* (1:1).

like, with the lobes incurved (1:1; 2:1; 3:1), with the leaf-surface rarely in a plane with the dorsal stem-surface; leaf-bases with 1-several cilia usually on postical base (occasionally lost), consisting of isodiametric cells (1:4). Ventral stem sectors wide (1:6) and with distinct underleaves (but these obsolete or absent in *attenuata* and *binsteadii*).[47] Gemmae commonly produced in some species (*attenuata, kunzeana*), rare in others, not limited to lobe-apices, the gemmiparous leaves often reduced.

The subgenus is exactly equivalent to the genus *Orthocaulis* of Buch (1933), and its chief distinguishing characters have been ably stressed by Buch. Buch also stressed the fact that the mode of origin of the leaf-lobes appeared to be different in *Orthocaulis* and *Barbilophozia*. In the present group the basic leaf-lobe number is two (as in most material of *kunzeana*), with a well-developed tendency for the ventral lobe to subdivide (resulting in a trilobed leaf with two small ventral lobes, contrasted to a larger dorsal lobe); occasionally (*O. quadrilobus*) the dorsal lobe may also be subdivided, resulting in a symmetrically four-lobed leaf. In *Barbilophozia*, on the other hand, the origin of the dorsal and ventral outer lobes appears to be from the basal cilia of the leaves, fide Buch.[48]

This subgenus is of an extremely synthetic nature and comes very close to the hypothetical common ancestral form from which the entire Lophozioid complex may have originated. The approach towards large underleaves and wide ventral stem-sectors (1:6), the lack of stability in the development of leaf-lobes (1:6; 3:1,4-11), the suberect or ascending growth, generalized form of the oil-bodies (2:7), unspecialized stem (1:5), and total lack of obviously derivative features all indicate a "low" position for *Orthocaulis*. Through *L. obtusa* the subgenus appears to be connected to the *Massula-Isopaches-Dilophozia* complex. Through *L. barbata* and *floerkei* it appears related to *Barbilophozia*. Through *L. Schultzii* and *heterocolpa* to *Leiocolea*. Through *L. quadrilobus* the subgenus is connected with *Temnoma*. Through *L. binsteadii* and *atlantica* it may be related to the *Anastrophyllum* complex (probably most directly to *A. saxicolus*). These annectant species are discussed more fully under their respective groups.

The subgenus is so closely related to *Barbilophozia* that Müller (1939, 1940, 1948) has refused to recognize it. The extremely close relationship is best brought out by a comparison between *L.* (*B.*) *barbata* (Plate 8, Figs. 1-6) and *L.* (*O.*) *atlantica* mod. *explanata-eflagellis* (Plate 8, Figs. 9-14). Such lax forms of *L. atlantica* may have much more strongly spreading leaves than normal gemmiparous, forms (compare 8:10,12 and 3:1), and may have occasional leaves 4-lobed (8:10,12), though most exhibit the normal *Orthocaulis* leaf-form (8:9,14). The clearest differences lie in the somewhat more

47 In the species with ability to produce discrete underleaves there is retention of wide ventral stem-sectors at least 8-10 cells wide. In *L.* (*O.*) *attenuata*, however, the ventral stem-sectors may be reduced to a width of 2 cell-rows (2:2).

48 This is readily apparent from studying poorly developed plants of *L. hatcheri* and *lycopodioides*. However, it is not evident in *L. barbata*, in my experience.

arched (and ventrally slightly decurrent) line of the leaf-insertion, which never is as semi-horizontal as in *Barbilophozia* (compare 8:5 and 9); in *Orthocaulis* the postical leaf-base is also slightly decurrent (8:9,12; 2:2,4), while it is non-decurrent in *Barbilophozia* (8:3); finally, the rhizoids form a usually denser ventral mat in *Barbilophozia* than in *Orthocaulis*. The effect of lengthening of the axis on the form of the leaf-insertion can be seen by comparing 2:4 with 8:9.

Buch (1933) divides the species into two sections, the *Stipulatae* (including *kunzeana, floerkei, quadriloba* and *atlantica*) and the *Exstipulatae* (including *attenuata* and *binsteadii*). This division appears unnatural in that *L. atlantica* is separated from *attenuata* and *binsteadii*, to which it is allied by a number of characters, as follows: ventral stem sectors narrow, reduced to a width of 4 or fewer cells, able to develop at best minute underleaves; leaves with postical margin unarmed by cilia, at most with a slime papillae that may be more or less stalked; shoots with gemmiparous leaves strongly inhibited in their development, remaining small, obscurely lobed, erect-appressed, and imbricate (forming more or less obvious erect, worm-like branches). For that reason I have reoriented the species into two different sections, as in the subjoining key.

KEY TO NEARCTIC SPECIES[49]

1. Plants unisexual; perianth free from bracts; leaf-sinuses acute to obtuse; cells normally collenchymatous: often with bulging trigones ..... 2.

2. Underleaves large, obvious, usually bifid and provided with 1-several cilia (1:6-7); leaves with postical bases occasionally or usually with 1-several cilia (1:4); cells of leaf-margin and leaf-lobes mostly 15-19 μ; gemmiparous plants with leaves not reduced; ventral stem-sectors 6-16 cells wide. *Sectio Kunzeanae* ..... 3.

3. Leaves largely or entirely 4-lobed for 1/2-2/3, the lobes narrowly triangular, with the margins (and especially the sinuses) distinctly reflexed ..... *L.* (*O.*) *quadrilobus.*

3. Leaves divided 1/3-1/2 into 2 or 3 broadly triangular to ovate lobes, whose margins and the sinuses between are scarcely reflexed (1:1,3,6,8) ..... 4.

4. Leaves all or mostly 2-lobed (1:1), the postical margin only very occasionally with a single basal cilium (1:6,8); leaves lobed about half their length (1:5,6); underleaves with each lobe with 1 or at most 2 cilia (1:6-8,10) ..... *L.* (*O.*) *kunzeanus.*

4. Leaves all or mostly 3-lobed, the postical base generally with 1-3 cilia; leaves

[49] Frye and Clark (1945, pp. 401-402) attempt a basic separation into species on the basis of number of leaf-lobes. This seems unfortunate, since the extremely closely related *atlantica* and *binsteadii* cannot be separated from each other on this basis. As is well known, the number of leaf-lobes in this group varies very widely with differences in nutrition and subsequent robustness of the plants. Frye and Clark (1945, p. 338) attempt to separate *Orthocaulis* from *Lophozia* (including *Massula*) on the basis of the interior cells of stem larger than cortical, vs. interior cells hardly larger than cortical cells (in *Lophozia*). In spite of the fact that there are numerous excellent separating characters, there is no constant difference between the groups in question (compare, for instance, the stems of *L.* (*Orthocaulis*) *kunzeana* (1:5) and *L.* (*O.*) *atlantica* (8:11) with that of *Massula obtusa* (9:8).

lobed merely 1/4-1/3 their length; underleaves with the lobes with several to many cilia on robust plants ..... *L.* (*O.*) *floerkei.*

2. Underleaves absent (2:2; 3:1) or present as occasional linear to lanceolate, undivided, obscure vestiges, never ciliate; leaves with postical bases never ciliate (2:2,6); gemmae usually on strongly ascending shoots with smaller, more or less reduced leaves; leaves largely 2-3-lobed for 1/4-1/2 their length; ventral stem-sectors reduced to a width of 2-5 cells wide usually (2:2). *Sectio Attenuatae* .... 5.

5. Plants with numerous slender, erect, filiform innovations bearing reduced, imbricate, appressed leaves and gemmae; gemmae green to pale brownish; leaves almost all 3-lobed, not or scarcely wider than long (2:1-2,4-6); sinuses descending 1/4-2/5, the lobes mostly slightly to distinctly longer than wide (2:5-6), occasionally ending in a row of two single cells (2:8); leaf-cells very small, 12.5-18 μ along margins of lobes (2:8); no underleaves, even on gemmiparous shoots (2:2) ..... *L.* (*O.*) *attenuata* (= *gracilis*).

5. Plants with stouter, erect, scarcely filiform innovations: the gemmae deep purple or reddish-brown, on relatively robust shoots (when present); leaf-cells larger, 16-25 μ along margins of leaf-lobes, often with bulging trigones (3:2) ..... 6.

6. Cells of leaf-lobes and leaf-margins 18-27 μ (3:2); leaves largely 3-lobed, the 3-lobed ones mostly distinctly wider than long, lobed 1/4-1/3 into broad, obtuse lobes that are considerably wider than long (3:4-11); frequently with minute underleaves (at least on gemmiparous shoots) .... *L.* (*O.*) *atlanticus.*

6. Cells of leaf-lobes and leaf-margins smaller, 16-19 μ; leaves largely 2-lobed, the 3-lobed ones not or scarcely wider than long, lobed 1/3-1/2 into narrow lobes that are slightly to distinctly longer than wide at base; underleaves absent (even on gemmiparous shoots) ..... *L.* (*O.*) *binsteadii.*

1. Plants bisexual, paroecious; perianths connate at base with bracts; leaves 2-lobed, the dorsal and sometimes ventral margins with a large triangular tooth; gemmae unknown; cells of leaf-lobes and margin 20-25 μ; underleaves present .... *L.* (*O.?*) *elongatus*[50].

Subgenus 2. BARBILOPHOZIA Lske. (emend. R. M. S.)

(Plates 7-8)

Large plants growing with stem decumbent, only the apex somewhat ascending; stems 11-15 cells high (7:1; 8:6), with medulla homogeneous (at most the ventral 1-2 medullary layers of cells smaller, but not forming a distinct mycorrhizal nutritive tissue). Rhizoids forming a dense ventral mat (8:1,5). Leaves nearly symmetrical, wider than long, normally 4 lobed, the dorsal and postical lobes smaller (occasionally merely forming large cilia: then leaf asymmetrical), apparently derived from marginal cilia (7:8; 8:1-3,5); leaf-insertion extremely oblique (as in *Leiocolea*), the leaves spreading horizontally and nearly flat (8:1,5); postical, and sometimes antical leaf-bases with 1-several long cilia (7:8) formed by notably elongate cells (different from *Orthocaulis*), but the cilia reduced to a stalked slime-papilla in *L. barbata.* Cells distinctly collenchymatous and thin-walled, with a generally papillose cuticle, small, about 25 μ (8:13); oil-bodies grayish, small, mostly 4-5 μ, nearly spherical, mostly 4-8 per cell, with the included oil-spherules numerous and clearly distinct. Ventral stem-sectors wide (8:3), developing distinct

50 This species more probably goes into the Section *Excisae* of *Dilophozia* (see footnote 80).

underleaves (7:3-4; 8:4-5) (minute or absent except on fertile shoots in *L. barbata*).[51] Gemmae very rare (except *L. hatcheri*), angular (7:2, 5-7). Perianths unmodified, plicate on their distal halves or more, gradually contracted to the mouth, which is not beaked. Sporophyte with seta of numerous rows of cells. Capsule-wall with 3-4 layers of cells, the inner with radial and tangential bands of thickening, the outer with radial (nodular) thickenings only. Dioecious. Antheridial stalk always biseriate.

The subgenus, as above emended, is equivalent to the genus *Barbilophozia* of Buch (1933). In other words, *Orthocaulis* is excluded from it. The chief differences between *Barbilophozia* and *Orthocaulis* have been stressed by Buch, so need not be detailed here.

Barbilophozia differs in general appearance from *Orthocaulis* to a considerable extent. The decumbent growth (forming low mats, rather than caespitose patches) is the most striking character separating the species in the field. The elongate cells of the cilia of the leaf bases is the best character separating the species from *Orthocaulis* under the microscope. Both subgenera agree in the nature and number, and size, of the oil-bodies, in the nearly isodiametric, rather small cells, and in most other features. They have therefore been reunited by Müller (1939, 1948). I feel, however, that they are distinct enough to warrant their subgeneric recognition.

Buch (1933) would derive *Barbilophozia* from *Leiocolea*. This suggestion has been criticized above, because it seems impossible to derive a relatively generalized type like *Barbilophozia* (with unspecialized perianths, unspecialized oil-bodies) from a highly derivative type like *Leiocolea* (in which the perianths and oil-bodies are extremely side-wise specialized).

KEY TO NEARCTIC SPECIES

1. Postical leaf-margin with 1-several cilia formed of elongate cells (7:8); leaf-lobes more or less distinctly mucronate-tipped (7.2,8); underleaves large, prominent, present throughout on sterile shoots; leaves obtrapezoidal: much wider near apex than near base. Sectio LYCOPODIOIDEAE ..... 2.

2. Leaves with apices (below points) largely margined by elongate cells; plants extremely large, 4-5 mm wide, yellowish-green; leaves very strongly rhombic, much broader distally than near base, divided into 3-4 very broadly triangular-ovate lobes more than twice as wide as long; gemmae usually absent; mouth of perianth ciliate-dentate with teeth mostly 2-3 cells long .....*L.* (*B.*) *lycopodioides*.

2. Leaves with apices of lobes margined with largely isodiametric cells; plants smaller, 1.5-2.2 mm wide, green to brownish-green; leaves usually less obviously rhombic (7:2) (occasionally strongly so, as in 7:8), divided into 3-4 triangular lobes less than twice as wide as long; gemmae reddish-brown, usually common (7:2,7); mouth of perianth shortly denticulate .....*L.* (*B.*) *hatcheri*.

1. Postical leaf-margin at most armed with a stalked slime-papilla or unarmed (8:1-3,5,9); leaf-lobes obtuse to merely acute (8:1-3); underleaves on sterile shoots

51 Even in *L. barbata* the ventral stem-sectors retain a width of 12-16 cells on robust plants that lack underleaves. In the other two species the ventral stem-sectors are at least that wide.

vestigial, occasionally rather distinct (8:1,4-5);[52] leaves nearly quadrate (when 4-lobed) and little wider distally than at base (8:1-3); gemmae very rare. Sectio BARBATAE ..... *L.* (*B.*) *barbata.*

Subgenus 3. LEIOCOLEA K. M.

Stems growing nearly horizontally, little ascending (except gemmiparous shoots of *L. heterocolpa*), but the shoot-apices with distinct dorsal autonomous curvature. Stems more than 10 cells high, with medulla entirely homogeneous, but with the lower 1-3 layers of medullary cells somewhat smaller than the dorsal medullary cells (5:8), but not forming a ventral mycorrhizal band; cortical cells able to develop distinctly thickened walls (usually in one cell-layer), slightly to scarcely smaller than the medullary (5:8). Rhizoids forming a dense postical mat (6:6). Ventral stem-sectors broad, mostly 6-12 rows of cells broad on sterile shoots and able to develop discrete underleaves (5:4-5; 6:8-12); in a few species (*L. badensis, turbinata*) the ventral stem-sectors only about 4-5 cells broad and unable to develop underleaves. Leaves very uniformly bilobed (5:1,6-7; 6:8), very obliquely inserted (appearing nearly horizontal laterally), scarcely concave to nearly flat (becoming somewhat dorsally convex in *L. rutheana*) (5:1; 6:7); postical leaf-margins unable to develop basal cilia (except rarely in *L. rutheana*). Leaf-cells large, mostly 35-50 μ in leaf-middle, strongly collenchymatous normally and with bulging trigones (5:3; 6:5), but sometimes thin-walled (6:4), with a generally very distinctly papillose to striolate-papillose cuticle (5:3, right-hand cell); oil-bodies grayish, very large, mostly 4-6 x 8-12 μ, or larger, mostly only 2-5 per cell, appearing somewhat opaque and formed of numerous very minute, scarcely distinct oil-globules that do not protrude (occasionally also with 1-several larger included oil-globules) (5:2-3; 6:4-5); chloroplasts averaging slightly to much smaller than the oil-bodies in size (5:3, 6:4-5). Gemmae absent (except *L. heterocolpa* and *harpanthoides*).

Dioecious or paroecious. Perianths slender, long, longly exserted tubular and terete, non-plicate, near apex swiftly constricted into a small, narrow beak (5:1; 6:6-7). Perichaetial bracts larger than leaves, but generally bilobed like leaves (6:6-7). Sporophyte with seta of numerous rows of cells (except *L. badensis*); capsule-wall 3, occasionally 3-4-stratose, the inner wall with annular (6:1), the outer with radial (nodular) thickenings (6:2). Antheridial stalks mostly biseriate.[53]

The subgenus as restricted above includes a closely related group of species. They agree in the nearly horizontal leaves with rather large, strongly collen-

52 Frye and Clark (1944, p. 426) attempt to separate *L. barbata* from the other two species because of the supposed absence of underleaves on sterile shoots. This is not strictly the case, as is evident in their Fig. 11 (p. 427), which is copied from Evans (1898), and shows a distinct underleaf on a sterile shoot. The underleaf in 8:4 also was taken from a normal sterile shoot.

53 In at least *L. gillmani* the antheridial stalk is very variable. In antheridia from one plant it varied from uniseriate (with 1-2 cells divided, thus locally biseriate), to completely biseriate, to triseriate near the distal end and biseriate near the base. Müller (1948, p. 14) however states "bei allen *Leiocolea*-Arten zweizellreihig."

chymatous cells, provided with peculiarly large oil-bodies, and a papillose cuticle. The stem-structure is uniform throughout the group, and the perianth is extremely characteristic (never recurring in such a form elsewhere in the genus). The group includes only one really divergent species-group (Sectio *Heterocolpae*) which approaches the ancestral form in the smaller leaf-cells, the less horizontal leaves and somewhat ascending growth as well as ability to produce gemmae. The other somewhat isolated species is *L. badensis*. This small species appears to be a reduced form, in which the seta has become reduced to a finite number of cell-rows, and in which there has been reduction of the ventral stem-sectors and total suppression of the underleaves. The species is also isolated in the thin-walled cells (with small trigones) whose cuticle is rarely distinctly papillose (6:4). Nevertheless, it would be absurd to consider such an obviously reduced, small form, as separate from *Leiocolea*.[54]

It is a moot question, answerable only on a personal basis, whether to consider *Leiocolea* as a subgenus of *Lophozia* or whether to separate it generically. If retained as a subgenus, it is certainly one of the most sharply circumscribed and most isolated subgeneric group in *Lophozia*. Its distinct relationship to *Barbilophozia* and *Orthocaulis* (on one hand) and *Massula*, on the other hand, however, make it wise to retain it as a subgenus, at least provisionally.

The genus is possibly related to *Dilophozia* through *Massula obtusa* (which Buch placed in *Leiocolea*), and also to *Barbilophozia* and *Orthocaulis* perhaps through *L. schultzii* (which has very large underleaves and occasionally shows a basal cilium on the postical leaf-base). Probably the first relationship is largely illusory and due to convergent evolution; the relationship to *Orthocaulis* (through a common form with *Barbilophozia*) is however unmistakable. The nearly horizontal leaf-insertion, papillose cuticle, large underleaves, etc., all indicate that the subgenus has a common ancestral form with *Barbilophozia* (which, however, had not yet developed the elongate cilia, nor the 4-lobed leaves). Such a form may have been extremely similar to *Orthocaulis kunzeanus*: but had already developed nearly horizontally inserted leaves.

Essentially, *Leiocolea* and *Barbilophozia* represent two related but largely independent evolutionary lines: the first a "lobe-reduction" line, the second a "lobe-development" line. The attempt to derive *Barbilophozia* (with its simple, plicate perianth and unspecialized oil-bodies) from *Leiocolea* (as done by Buch, 1933), seems to the writer to lack logic. If anything, the opposite derivation seems decidedly more plausible.

The subgenus, in all of its characters, except the primitive stem-structure, retention of underleaves, and papillose cuticle, represents a decidedly spe-

54 Analogously, it seems scarcely warranted to me to consider the small, reduced species *"Sphenolobus" hellerianus* as generically separated from *Sphenolobus minutus*. In both cases it has been obvious that there has occurred parallel reduction in size, correlated with reduction in number of rows of the cells of the axis of gametophyte and sporophyte.

cialized entity, both in positive ways (leaf insertion; fixed number of leaf-lobes; perianth form; oil-body form, etc.) as well as in negative ways (loss of gemmae, etc.).

KEY TO NEARCTIC SPECIES

1. Paroecious (5:1; 6:7). Plants large, 1.8-5 mm wide x 2-8 mm long; gemmae absent; underleaves distinct throughout (5:4-5; 6-8); cells of the leaf-middle mostly 32-36 x 38-48 μ, of the leaf-apices 25-30 μ, with large to bulging trigones (5:3; 6:5) ..... 2.

2. Leaves dorsally convex, widest basally and wider (to 3 mm) than long, ventrally more or less decurrent (5:1,6-7); underleaves extremely large, ciliate (some more than half as long as leaves) (5:4-5); plants 3-5 mm wide x 4-8 cm long ..... *L. rutheana*[55].

2. Leaves flat or slightly dorsally concave, widest in middle and longer than wide (at most 1.6 mm wide), ventrally not decurrent (5:6-8); underleaves small, inconspicuous (6:8-12); plants 1.8-2.8 mm wide x 2-4 cm long ..... *L. gillmani*[56]

1. Dioecious ..... 3.

3. Underleaves present; cuticle usually distinctly papillose; leaves with generally distinct to bulging trigones; plants larger, more robust, 1-4 mm wide x 0.8-8 cm long ..... 4.

4. Gemmae present at the leaf-apices (generally on more or less erect shoots with erect or appressed, often reduced leaves); leaf-cells with large, bulging trigones (often yellowish), 25-30 μ in leaf-middle, or smaller; plants small, 1-2 mm wide x 2-25 mm long; usually sterile ..... 5.

5. Gemmae common, brownish; cells of leaf-apices 18-20-25 μ, in leaf-middle to 30 μ, with walls between trigones thin; leaf-sinuses acute to rectangular, 1/4-1/3 the leaf length ..... *L. heterocolpa.*

5. Gemmae reddish-purple; cells 15-24 μ, with thickened walls and very large, bulging yellow trigones; leaf-sinuses crescentic or lunate, only 1/6-1/4 the leaf-length ..... *L. harpanthoides.*

4. Gemmae constantly absent: the plants strongly horizontal in growth, with nearly horizontal, spreading leaves; leaf-cells with minute or moderate (never strongly bulging) trigones, 25-30 x 30-40 μ or larger in leaf middle; cortex of stem with thin hyaline walls; leaves not or scarcely concave; plants often larger, 1-4 mm wide x 1-8 cm long ..... 6.

6. Cells in leaf-apices 30-35 μ, in leaf-middle 35-40 μ, plants large, 2.5-4 mm wide x 2-8 cm long; leaves usually more or less dorsally convex; spores 12-15 μ; female bracts with lobes entire ..... *L. bantriensis.*

---

55 According to Frye and Clark (1945. p. 380) *L. rutheana* is separated from *harpanthoides* by the "thin and colorless" walls of the leaf-cells. In much material seen (among it especially plants from Bergen Swamp, N. Y.) the very large, bulging trigones of *L. rutheana* were a deep golden brown. Since Frye and Clark state they have seen no specimens of either species, their separation can scarcely be based on actual observations.

56 Frye and Clark (1945, p. 380) separate *L. gillmani* from *mülleri* because its trigones are supposedly "small" (compared to "medium large to bulging" for *mülleri*). There is no separation between the two species in this regard, and *gillmani* often has large bulging trigones (see, for instance, 6:5). Using the criteria in the above key, the *L. schultzii* var. *laxa* Schiffn., described from England, would fall under *L. gillmani*, and appears to be a marl-bog form of the latter species. I believe the variety to be better placed as *L. gillmani* var. *laxa* (Schiffn.) comb. n. Macvicar (1926) illustrates and describes this anomalous variant.

6. Cells in leaf-apices 25 μ, in leaf-middle 25-30 μ wide; plants smaller, 1-2.8 mm wide x 1-4 cm long; leaves not convex; spores 10-12 μ; female bracts usually with lobes denticulate ..... *L. mülleri.*

3. Underleaves lacking throughout; cuticle smooth or nearly; leaves with thin walls and slight or no trigones (6:4); plants small, mostly 3-8 mm long, 0.6-1 mm wide; cortical stem cells thin-walled, hyaline, 2-4 times as long as wide; cells 30-35 μ in lobes, 32-38 μ wide in leaf-middle; gemmae absent ..... *L. badensis.*

Subgenera 4-6. MASSULA — ISOPACHES — DILOPHOZIA:[57]

INTRODUCTION

In the critique (p. 20) I have demonstrated that *Massula* and *Isopaches* (as they stand in the literature) are not homogeneous and natural units, and that both are intimately related to *Dilophozia*. These three subgenera have in common several features that separate them from the previous three subgeneric groups, as follows: 1. More or less uniformly bilobed leaves (again found in *Leiocolea*). 2. Total absence of underleaves.[58] 3. Development, in many species of a dorsiventral modification of the stem medulla. 4. Cuticle of leaf-cells not or slightly papillose. 5. Leaf-insertion oblique (again found in *Orthocaulis*). 6. Leaf-bases never ciliate.

In contrast, the leaves are mostly 3-4-lobed in previous subgenera (except *Leiocolea*), distinct underleaves are retained in most species of each subgenus (together with wide ventral stem sectors), the cuticle is papillose except in hygrophytic modifications, and the leaf-bases are usually ciliate at the postical bases (not so in most species of *Leiocolea*).

The three subgenera I recognize in this complex were placed as members of the subgenus *Dilophozia* in most recent works (Müller, 1911; Macvicar, 1926; Meylan, 1924). They differ, however, in several fundamental ways, chiefly: 1. In the number of layers of the capsule-wall, and the nature of their thickenings. 2. The stem-structure. 3. The size and number, and relative homogeneity of the oil-bodies. 4. The ability (or lack of ability) to develop trigones or thick-walls of the leaf and stem-cells. 5. The relative width of the ventral stem-sectors.

On the basis of these characters, these subgenera may be separated.[59] These subgenera and their relationships are discussed in more detail

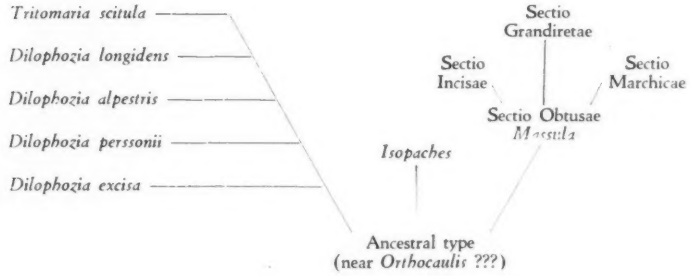
---

57 The present complex of three subgenera has been so differently treated by various workers, and appears so closely interrelated, that its treatment as a unit seems necessary, before the several subgeneric groups are individually treated.

58 In *Massula*, however, the ventral stem-sectors remain broad, and are able to produce relatively large and ciliate underleaves in at least one species (*L. obtusa*). See in this connection the following discussion, and the discussion under *Massula*.

59 See key to genera and subgenera, p. 33.

individually (p. 50 to 62). For the present, their relationship can be diagramatically expressed as follows:



It is not to be presumed from the above diagram that any of the existing species gave rise to any other existing form: *L. excisa* did certainly not give rise to *T. scitula*. But it is attempted to indicate that *L. excisa* has been developed from a form ancestral to the *L. alpestris-T. scitula* developmental line. Furthermore, much of the above diagram indicates only morphological similarity and is not intended to portray a strict phyletic history for the complex. If such is portrayed it is, to some degree at least, accidental.

Several distinct relationships appear to be indicated, as follows:

a. *L. perssonii* appears related to other species of *Dilophozia* through the *L. alpestris-wenzelii* complex: the similarity in the circular, very shallowly divided leaves, and in the brownish gemmae-color is suggestive.[60]

b. *Tritomaria scitula* appears to connect *Eutritomaria* to the Sectio Ventricosae of *Dilophozia*: the rectangular leaf-shape and the acute, narrow leaf-lobes, the angular leaf-sinuses, as well as suberect growth of the *longidens* subsection indicate a direct relationship.

c. There is some relationship, though not very close, between *Lophozia excisa* and *Isopaches bicrenata* (perhaps through a common ancestral type, as pictured). The closeness of the relationship is much less than has been previously pictured in the older literature (the stem-structure, structure of the capsule-wall, and other characteristics indicate a superficial convergence more than a real relationship). The leaf-type, cell-size, oil-body form, paroecious inflorescence, leaf-insertion, dentition of male and female bracts results in a startling similarity.

d. Any relationship between *Isopaches* and *Massula* must be quite distant. The reduction of the capsule-wall in *Isopaches*, and the specialization of the

60 Also suggestive is the fact that the Sectio *Excisae* (i.e., *excisa* and *perssonii*) develop denticulate leaf-margins, with gemmae-formation; this is also the case with *L. alpestris* (18:1), but is not the case with the other species of the Sectios *Longidentae* and *Ventricosae*, or *Tritomaria*.

outer layer, as well as the reduction in stem-size, all indicate *Isopaches* is a reduced type, and as such cannot serve as an ancestral form for *Massula* (where the capsule wall is 3-5 stratose and the stem also correspondingly thicker). In the unspecialized oil-bodies *Isopaches*, however, approaches much nearer the ancestral type than does *Massula*.

In attempting to arrive at some reasonable arrangement of the *Lophozia* groups with bilobed leaves, one is reduced to looking for an "archetype" below the *Isopaches bicrenatus-Dilophozia excisa* complex. The entire *Dilophozia* complex can scarcely be considered in this connection because of the very specialized nature of the medulla of the stem. Similarly, *Massula* cannot come under consideration because of the very specialized nature of the oil-bodies. In some features *I. bicrenatus* approximates the ancestral form most closely. However, the reduced 2-layered wall of the capsule and the small stem are obviously secondary features which preclude considering *Isopaches* as directly ancestral.

It is thus evident that all of the subgenera here considered (*Dilophozia*, because of the medulla; *Massula*, because of the oil-bodies; *Isopaches*, because of the reduced capsule-wall) are derivative in one or several ways.

A further indication of the absence of an archetype is the fact that such an archetypal form would have to show some approximation to the ancestral *Orthocaulis*-like complex. It must be stressed that there is no species that can be considered truly intermediate to either *Orthocaulis* or *Leiocolea* or *Barbilophozia*. The two-lobed species of *Lophozia* thus are rather clearly isolated, and could perhaps be considered as a discrete genus. Any connection with *Orthocaulis*, *Barbilophozia* or *Leiocolea* (such as is indicated by *L. obtusa*) may very well be due to convergence, and thus be simulated rather than real. If this should prove to be the case it may well be desirable to follow Buch (1941) in his circumscription of *Lophozia* (including *Isopaches*, however).

Subgenus 4. MASSULA K. Müller emend. K. M. S.

Plants moderate-sized, growing with stems horizontal or slightly ascending (10:1). Stem flattened (9:8; 10:9; 12:1), 12 or more cells high, with medulla of large, thin-walled, hyaline cells, the cells of the ventral layers as large (12:1) or even a little larger (10:9; 11:5) than those of the dorsal layers; the cortical cells thin-walled or nearly (11:5; 12:1,3; 9:3), scarcely differentiated from the medullary: cortical layer occasionally with slight mycorrhizal infestation (12:1), but the ventral medullary layers completely free of mycorrhiza. Rhizoids forming a very dense ventral mat (10:1). Leaves more or less spreading laterally, symmetrically bilobed, but often in part 3-4-lobed (9:1,4,6; 10:2-6), often undulate (12:4-5) occasionally with more or less distinct marginal teeth (9:6; 10:4,11; 10:10; 12:5) (always more distinct on perigonal and perichaetial leaves); leaf insertion oblique (10:6; 12:6), sometimes very much so and approaching horizontal (*L. obtusa*) (9:1); leaf-bases never ciliate. Cells non-collenchymatous (9:2; 11:1-2,8),

usually extremely thin-walled (becoming somewhat equally thick-walled in *L. grandiretis*), generally large (mostly 35-60 μ) and non-papillose; oil-bodies colorless, hyaline, very strongly refractive, nearly or quite homogeneous within and smooth appearing externally, usually very small (2 μ) (11:8; 12:7), but up to 5-8 μ in *L. grandiretis* (where often double) (10:7-8), very numerous, mostly 30-60 per cell. Ventral stem sectors mostly 6-12 cells wide, mostly lacking ability to develop underleaves.[61] Gemmae commonly produced, ovoid and smooth or angulate, to stellate, their formation usually limited to the youngest leaves (resulting in the formation of apical gemmae-masses (10:1; 11:4)).

Perianth unmodified, plicate distally, not beaked (11:9). Sporophyte with seta of many rows of cells; capsule-wall 3-5 stratose, the inner layer with complete tangential and radial bands (with annular thickenings), the outer with radial thickenings only (e.g., with "nodular" thickenings). Dioecious or paroecious.

The subgenus *Massula* differs from the other two related subgenera chiefly in the very numerous oil-bodies that appear to be nearly or quite homogeneous within (hence lacking distinct oil-globules or spherules),[62] and in the entirely homogeneous nature of the large-celled medulla of the dorsiventrally flattened stem.[63]

In addition, the cells in this subgenus are always non-collenchymatous, and are relatively large in most species.

The relationships of Massula have been discussed in connection with the following two subgenera on p. 48. In that connection, the classification of the subgenus was also mentioned, and need not be repeated here.

Species: Lophozia grandiretis, L. incisa, L. jenseni, jurensis, kiaeri, marchica, mildeana, opacifolia, violascens, obtusa.

The subgenus is divided in the following key into four sections. These are here established as homogeneous units, it is believed. Some may question

---

61 The very wide ventral stem-sectors of *Massula* are a primitive characteristic which ally it with the previous three subgenera (*Orthocaulis, Barbilophozia, Leiocolea*), and separate it from the next two subgenera (*Isopaches, Dilophozia*). In all of the species the ventral stem sectors have "lost" the ability to develop discrete underleaves (in spite of their great width), except in *L. obtusa*, in which normal sterile shoots have occasional underleaves that are ciliate and very well developed (much as in the preceding subgenera).

62 Müller (1939) stressed the small size of the oil-bodies as a generic character. As is evident in 10:7-8, of *L. grandiretis*, the oil-bodies may be up to 5-6 μ (when simple) or 6-8 μ (when double). Hence I believe the homogeneous nature, and the large number of the oil-bodies are more characteristic than their size.

63 The stem structure appears fundamental to me, on a subgeneric basis. Therefore I would exclude *L. excisa* and *perssonii* from *Massula*, and return these to *Dilophozia*, in which they fit better because of the dorsiventrally differentiated medulla. These two species may also have the oil-bodies relatively non-homogeneous, rather distinctly granular in appearance, and relatively fewer than in *Massula* proper. In the oil-bodies, in my estimate, they belong fully as much in *Dilophozia* as in *Massula:* hence I believe the stem-structure may well be the deciding factor.

the inclusion of *L. obtusa* in *Massula* (as has Buch, 1942). However, the stem-structure of *L. obtusa* agrees with *Massula*, s. str., as do the numerous oil-bodies, and the cellular structure in general. The tendency to develop small trigones is somewhat at variance with the other species (but even *L. incisa* may develop trigones in the var. *inermis* K. M.). Perhaps the two most important characters that isolate *L. obtusa* from the other species of *Massula* are the often slightly papillose cuticle, and the 5-stratose capsule wall. In the other species of *Massula* (and in all other species of *Lophozia* with bilobed leaves) the cuticle is smooth, and the capsule-wall is never more than 4-stratose, in my experience.

L. obtusa has remained one of the most critical species in the complex. It was placed in *Leiocolea* by Buch (1933), in which he was followed by Frye and Clark (1944), who, however, saw no material of it. It had been previously placed by Warnstorff (1903) in the species of *Lophozia* now segregated as *Leiocolea*, and by Müller (1910) in the *Orthocaulis* section of the subgenus *Barbilophozia* (s. lat.). None of these positions were at all satisfactory, as Müller (1939) indicated, placing the species in a novel position: within the subgenus *Massula*, of *Lophozia*. Meylan (1939) also attacked Buch's disposition of the species, and suggested it was related most closely to *Barbilophozia barbata* (and should perhaps be placed in a separate subgenus with the latter). Buch (1942) again reiterated his belief that on the basis of stem-structure the species belonged in *Leiocolea*, and not in *Lophozia* (incl. *Massula* and *Dilophozia*), but conceded it might be best to separate it subgenerically from *Leiocolea* (as the subgenus *Obtusifolium* Buch).

This, to the present writer, is not at all necessary. I have studied material of the species from Michigan and from Germany (Feldberg, Baden, leg. K. Müller), and find that in stem-structure, leaf-form, type of leaf-insertion, etc., the species agrees quite closely with *Massula*. In fact, I believe the species is probably related most closely to *L. grandiretis*. It agrees closely with the latter in the wide leaves with obtuse lobes. The reflexed or gibbose sinuses are highly reminiscent of *L. marchica*. Although the smaller cells seem to separate the species from our other *Massula* species, it must be remembered that two of the arctic alpine species that certainly belong in *Massula* (*L. violascens*, but especially *L. jenseni*) have the cells no larger. *L. obtusa* therefore does not occupy a more isolated position in *Massula* than do such species as *L. grandiretis* or *L. incisa*. (I cannot very seriously take the suggestion (Andrews, 1948) that *L. incisa* should go into a discrete subgenus, by itself, since that species and *L. grandiretis* are rather distinctly allied. *L. incisa*, however, is somewhat isolated from the other *Massula* species in that the leaves are unusually narrow and only on very robust shoots as wide or wider than long). *L. obtusa* is, admittedly, a synthetic species. It is the only member of the *Massula-Isopaches-Dilophozia* complex which retains the ability to develop underleaves; it is the only species of *Massula* which retains the ability to develop small trigones and a papillose cuticle; it also retains relatively small leaf-cells (and is closer to *Orthocaulis* than *Massula* in this regard).

Like the other *Massula* species, it retains wide ventral stem-sectors, and wider than long leaves that regularly retain the ability, on robust shoots, to develop 3-4-lobed leaves, or marginal teeth. In all of these characteristics *L. obtusa* approaches *Orthocaulis* (with the species of which it was associated by Müller in 1910). The leaf-shape of *L. obtusa*, with the somewhat reflexed sinuses, approaches very closely *L.* (*Orthocaulis*) *kunzeanus:* a species which both Buch (1933) and I consider as extremely archaic and reminiscent (at least) of the archetype of the Lophoziaceae.

L. obtusa, therefore, stands far below the other species of *Massula*, and indicates a clear derivation of *Massula* from *Orthocaulis* (almost certainly quite independent of the *Dilophozia-Tritomaria-Saccobasis* developmental lines). It may therefore be found advisable to eventually separate *Massula* generically from *Lophozia* (especially if the more radical scheme on p. 30 is accepted.)[64] However, *L. obtusa* has acquired the non-collenchymatous leaf-cells, the numerous minute oil-bodies and the nearly horizontal leaf-insertion of *Massula*, together with the flattened stem, with the cortical cell-layers unable to produce thick walls. For that reason the disposition of *L. obtusa* in *Massula* is well established.[65]

Meylan (1939) has argued that *L. obtusa* is related to *L. barbata* possibly because of the retention of underleaves and because of the extremely oblique leaf-insertion. In some ways it stands between *Barbilophozia barbata* and the more typical species of *Massula*. The ability to develop a papillose cuticle and retention of the ability to develop small trigones of the leaves, as well as the retention of the ability to develop underleaves are all characteristic of *Barbilophozia*. The occasional leaves that show a divided ventral lobe, or a discrete lobe-like antical tooth of *L. obtusa* heighten this general similarity. However, the oil-body structure, the thin-walled cells of the stem, the relatively non-collenchymatous cells, the rather flattened stem, and the leaf-form all argue that *L. obtusa* go into *Massula*.[66]

---

64 On a phylogenetic basis a good argument could be made in favor of accepting a genus *Lophozia* (including *Dilophozia, Tritomaria, Saccobasis*) discrete from a genus *Massula*. It is only the existence of the annectant *Isopaches* (with the stem-anatomy nearer *Massula*, the oil-bodies as in *Dilophozia*) that makes such a treatment difficult.

65 When Buch (1942) reiterated his belief that *L. obtusa* should go near or in *Leiocolea* he obviously overlooked the fact that all species of *Massula* have the stem-structure characteristic of *L. obtusa*. The thick-walled cortical cells of *Leiocolea*, the collenchymatous leaf-cells, the large oil-bodies, the inability to develop 3-lobed or dentate leaves, as well as the obviously specialized perianth indicate that *Leiocolea* represents a distinct developmental line whose sole possible relationship to *Massula* lies through the hypothetically ancestral *Orthocaulis*.

66 Phylogenetically these similarities between *L. obtusa* and *L. barbata* mean merely that the two species have had a common ancestral form (*Orthocaulis*). The wide ventral stem-sectors, ability to produce underleaves, tendency to produce occasional or frequent supplementary leaf-lobes are all characteristics that, in my estimate, represent retention of archaic characters or atavistic tendencies. In both groups there has been apparently independent development of a more oblique line of leaf-insertion.

The frequent occurrence of discrete underleaves (e.g., the retention of the ability of the ventral stem-sectors to develop underleaves) in *L. obtusa* is a strong argument in favor of not separating the *Orthocaulis-Barbilophozia-Leiocolea* complex generically from *Massula* and *Dilophozia* (as was suggested by Buch, 1942, and as has been accepted by Müller, 1948). Since stem structure offers no separation between these groups, the relative width of the ventral stem-sectors (and consequent ability to develop underleaves) seems the most valid criterion for a division into two major groups (see p. 33). *L. obtusa*, however, represents an intermediate type. Though it belongs to the *Dilophozia-Massula* complex, which normally lacks the ability to produce underleaves, it often has small underleaves (hence approaches the *Orthocaulis-Barbilophozia-Leiocolea* complex in this criterion). Since neither stem-structure, nor underleaf development therefore allows a clear-cut separation, no generic division appears warranted.[67]

KEY TO NEARCTIC SPECIES

1. Gemmae angulate to stellate (10:10; 11:7) greenish (walls not pigmented); leaves with occasional to many fine marginal teeth (or lobes broadly rounded at apex) (9:1,4,6-7; 10:2 4,11). Arctic-alpine to Subalpine species ..... 2.

2. Leaf-cells smaller, 23-30 μ in leaf-middle; leaves normally only 2-lobed, with the lobes obtuse to rounded (9:5,4,7),[68] separated by an acute, gibbous sinus; cuticle often slightly papillose; underleaves occasionally well-developed on sterile shoots (9:4-5); dorsal cortical cells somewhat smaller in diameter than medullary (9:8); leaves slightly to distinctly wider than long, extremely obliquely inserted (9:5); gemmae rare; stems slender and leaves distant (9:4). Sectio OBTUSAE ..... *L.* (*M.*) *obtusa*.

2. Leaf-cells large, 30-60 μ in leaf-middle; leaves occasionally or frequently with supplementary marginal lobes or teeth (10:3,11; 11:5,9); leaf-lobes subacute to acute or apiculate (10:2-4,11; 11:10), more rarely obtuse (11:1), the leaf-sinuses not gibbous; cuticle smooth (11:4); underleaves uniformly absent; dorsal cortical cells equal to medullary in diameter (10:9; 11:5); leaves moderately obliquely inserted, dorsally often little oblique (10:1,6; 11:6); gemmae abundant, stems thick and fleshy, leaves imbricate (10:1; 11:6) ..... 3.

3. Leaves much wider than long, lobed 1/5-1/3 into 2-3 subacute or obtuse lobes with few or no marginal teeth (10:2-6,11); plants moderately chlorophyllose, pure-green, often reddish to reddish-black where exposed; stem ventrally brownish to purplish (11:3), the pigmentation often extending over entire stem and leaves; leaf-cells 50-60 μ in leaf-middle (11:2); oil-bodies spherical, 4-5 μ, occasionally twinned and 4 x 6-8 μ; perianth short, scarcely exserted; subcalciphyte. Sectio GRANDIRETAE ..... *L.* (*M.*) *grandiretis*.

3. Leaves not or scarcely wider than long, lobed ½ their length, with narrow lobes usually provided with spinous teeth or supplementary lobes (11:6,-

---

67 The intrageneric variation in retention of wide ventral stem-sectors (and generally correlated ability to develop underleaves) is expressed graphically in Diagram I (p. 83). This clearly indicates why a division of *Lophozia* (s. lat.) into "genera" cannot be accomplished on this basis.

68 The difference in leaf-form between the sectio *Obtusae* and the sectio *Incisae* occasionally vanishes when extreme forms are examined. Leaves of *L. obtusa* may become sharply pointed and provided with several fine marginal teeth on non-gemmiparous sterile shoots: much as in *L. grandiretis* (compare 9:6 with 10:4,11).

10);[69] plants opaque, densely chlorophyllose, bluish-green throughout, the cell-walls never pigmented; leaf-cells 30-35 μ in leaf-middle (11:8); oil-bodies ovoid to subspherical, 2-3 μ, never twinned (11:8); perianth long, obviously emergent (11:9); extreme oxylophyte. SECTIO INCISAE .... *L.* (*M.*) *incisa.*

1. Gemmae ovoid, lacking protuberances; leaves lacking marginal teeth usually, the lobes acute to obtuse (12:4-5). (Cortical stem-cells 4-8 times as long as wide, mostly merely half as wide as basal leaf cells; or gemmae purplish). Sectio MARCHICAE ..... 4.

4. Gemmae greenish, scarcely forming globular masses at the stem-apices (12:4); cortical stem-cells 4-8 times as long as wide, only circa half as wide as basal leaf cells (12:2-3); cells of leaf-middle large, 40-50 μ; leaves extremely variable, flaccid and undulate, 2-5-lobed, the lobes usually acute (12:4-5). Subtropical to Subarctic species (rarely in the Arctic) ..... 5.

5. Plants totally green, except for the deeply purplish pigmented ventral side of the stem and rhizoids;[70] perianths green throughout; perianth-mouth denticulate with short, 1-celled teeth; plants flexuous and flaccid, the leaves strongly undulate (12:4); gemmae about 16 μ; only in bogs .....*L.* (*M.*) *marchica.*

5. Plants and perianths largely reddish-tinged, but the postical side of stem not purplish, green; perianth-mouth denticulate with teeth largely 2-3 cells long; plants scarcely flexuous, the stems more rigid, the leaves not flaccid, somewhat undulate; gemmae about 20-25 μ; usually on moist, sandy, acid soil .....*L.* (*M.*) *mildeana.*

4. Gemmae purplish, often forming distal terminal masses (as in 10:1); cortical stem-cells 2-4 times as long as wide, not or little narrower than basal leaf-cells; cells of leaf-middle 20-35 μ; leaves nearly uniformly 2-lobed, lacking marginal teeth. Arctic-alpine ..... 6.

6. Cells larger, 30-35 μ in leaf-middle, 25-30 μ in leaf-lobes; leaves scarcely wider than long, to 1/3 bilobed; lobes acute to obtuse .....*L.* (*M.*) *violascens.*

6. Cells smaller, 20-30 μ in leaf-middle, 18-26 μ in leaf-lobes; leaves distinctly wider than long, about 1/4 lobed, the lobes obtuse to rounded at apex ....*L.* (*M.*) *jenseni.*

In the above seven Nearctic species of *Massula* I have not been able to demonstrate the presence of a homogeneous stem-medulla in the Arctic-alpine *L. violascens* and *jenseni*, since I have seen no material of these. They belong almost certainly in *Massula* sectio *Marchicae*, since they share with *L. marchica* the ovoid gemmae, the wider than long leaves, the non-collenchymatous leaf-cells, and relatively thin-walled cortical cells, as well as a general similarity in facies. All of the species placed in *Massula* (including the European *L. jurensis* and *opacifolia*, of which I have seen examples, and *L. kiaeri*, which is close to *grandiretis*) agree in having a distinct habitus. They are, in general, more fleshy and flaccid plants than the species of *Dilophozia;* they have more

69 Well-developed plants differ at once from other Lophoziaceae in the numerous spinous marginal teeth. In the plant in 11:6,9, the var. *inermis* K. M. is figured, which represents a reduced form with few or no marginal supplementary teeth or lobes (11:10) and with distinct trigones. Juvenile plants of typical *incisa* approach this condition.

70 The totally green color of the leaves has been stressed in the literature as separating *marchica* from *mildeana*. This character must be used with caution, since in some material of *marchica* I have collected (St. Louis Co., Minnesota), the purplish pigmentation extends to the basal halves of the leaves.

wavy, broader leaves (broader than long in all but *incisa*), with very thin-walled cells; they have the gemmae (where produced in abundance) at the shoot-tips, in large masses. This latter characteristic seems important. The ability to produce gemmae seems limited to the embryonic leaves, hence is localized near the shoot-apex, resulting frequently in large terminal masses of gemmae (10:1) while the older leaves, as they approach maturity seem to lose the ability to produce gemmae. In *Dilophozia* this is not the case. The gemmae-production, though initiated before maturity of the leaves, continues until the leaves have attained their full size; hence gemmae occur in obviously individual masses at the lobe-apices of the individual leaves of the younger portions of the stems (15:1,6; 18:1).

Perhaps one of the most valuable criteria for distinguishing *Massula* from related subgenera is the fact that the ventral stem-sectors in *Massula* are well-developed (much as in the *Orthocaulis-Barbilophozia-Leiocolea* complex) and generally at least 6-12, often 16 cells broad. In *Isopaches* and *Dilophozia* the ventral stem sectors are very narrow and generally only 2-3 cells (more rarely 4 cells) wide. In the narrow ventral stem-sectors *L. excisa* agrees with *Dilophozia* (as it does in stem-structure); hence I would place that species in *Dilophozia* (rather than in *Massula*, where Müller, 1939, places it). In one species of *Massula* (*obtusa*) the wide ventral stem-sectors still retain the ability to develop underleaves on sterile shoots.[71]

Subgenus 5. ISOPACHES Buch, emend. K. M.

This subgenus includes only two species, and may be separated as follows:

Plants small or medium sized, 5-12 mm long, growing with apex strongly ascending, the older portions closely prostrate. Stem merely 8-10 cells high, with medulla of large, somewhat thick-walled uniform cells not attacked by mycorrhiza,[72] the ventral layers of cells as large as the dorsal layers (13:8); cortical cells little different from medullary, thick-walled. Rhizoids forming a moderately dense ventral mat (13:8). Leaves more or less erect or erect-appressed, imbricate, never horizontally spreading, nearly symmetrically bilobed (never 3-4 lobed), orbicular, somewhat concave (13:7), the leaf-margins entire (except on gemmiparous shoots) (13:1); leaf-insertion oblique, but not strongly so (13:7), the leaves appearing somewhat transverse; leaf-bases never ciliate. Cells strongly and equally pachydermous, the lumens appearing guttulate, non-collenchymatous, small, about 25-32 μ in leaf-middle (13:3-4);

71 These are quite frequently present, but hidden among the dense rhizoid-mat on older shoots. On the younger parts of the plants they are often very obvious and strikingly similar to those of *L. barbata*. Underleaves occur with about equal frequency in both these species, are about equal in size, and equally difficult to demonstrate. Frye and Clark (1945) state that in *obtusa* the underleaves are present "where stems fork, elsewhere wanting or rudimentary."

72 The ventral cortical cells (especially the rhizoid-initials) are early attacked by mycorrhiza and the cortical infection often extends to the medullary layer of cells immediately above (as in 13:8).

oil bodies distinctly grayish because of the numerous distinct included oil-globules, little refractive, appearing granulate externally (13:3), moderate in size, (mostly 4-5 μ), mostly 6-12 per cell (*e.g.*, as in *Dilophozia*); absent from marginal cells (13:4). Ventral stem-sectors obsolete, never producing underleaves. Gemmae angulate-stellate, common (13:5), gemmiparous leaves becoming strongly dentate (13:1).

Perianth unmodified, gradually narrowed to the ciliate mouth (13:6), not beaked. Sporophyte with seta of many rows of cells (often reduced to 16 external rows in *L. bicrenata*).[73] Capsule-wall 2-stratose (rarely 3-stratose in *bicrenata*), the inner and outer layers both with incomplete tangential and complete radial thickenings (*i.e.*, both with semi-annular thickenings) (13: 10-11.) Paroecious or dioecious.

Isopaches (after the exclusion of *I. hellerianus*) stands in some ways between *Massula* and *Dilophozia*. Like the former, the medulla of the stem is unspecialized and the leaf-cells are non-collenchymatous; like the latter, the oil-bodies are few in number, generally larger, and not at all homogeneous within, nor as highly refractive in appearance. *Isopaches* cannot be considered as truly annectant between the two subgenera, however, since it has been sidewise specialized in the reduced capsule-wall (normally bistratose), as well as in the development of only partial thickenings of the tangential walls of the outer layer. The two included species are also in general more xeromorphic than the other species of the complex, as is obvious from the guttulate cell-net and the most often closely imbricate leaves.

Species.—*L. bicrenatus, L. decolorans.* Only *bicrenatus* occurs in North America.

Subgenus 6. DILOPHOZIA K. M. emend. R. M. S.

The subgenus *Dilophozia*, as accepted here, may be circumscribed as follows:

Moderate-sized or small plants, 8-60 mm long, generally decumbent in growth with ascending apices (strongly ascending in growth in *longidens* and *gracillima* only) (15:1). Stem 10-16 or even 22 cell-layers at maturity, distinctly dorsiventrally differentiated: the ventral 0.5-0.7 of the medulla consisting of small, narrow cells, soon largely destroyed by mycorrhizal activity and becoming brownish, the upper third or half of the medulla of large, thin-walled hyaline or chlorophyllose cells; cortical cells similar to medullary (14:7) or differing from medullary chiefly in the slightly thicker walls (17:8), similar to medullary in size (in cross-section). Rhizoids forming a dense ventral mat (15:6; 17:2). Leaves obliquely inserted (almost subtransversely dorsally in *longidens* and *gracillima*), obliquely spreading and not or little imbricate, almost uniformly bilobed and with entire margins, the postical base never ciliate (15:1,6; 16:4; 18:4). Cells strongly bulging trigones, (15:3;

[73] The seta is supposed to be formed of 16 epidermal rows of cells, *fide* Buch (1933, 1942). As is evident from 13:9, there may be up to 21 outer cell-rows. *Isopaches* thus does not differ from *Dilophozia* in this regard (compare 13:9 with 14:4).

16:3,5; 17:4)[74] rather small (25-32 μ mostly in leaf-middle); oil-bodies grayish, little refractive, non-homogeneous, including numerous small, more or less protuberant oil-globules (thus appearing granular to coarsely papillose externally), moderate in size (mostly 4-5 μ), and moderate in number, mostly 8-20, rarely to 25 per cell (14:2; 16:3,5; 17:4). Ventral stem-sectors obsolete, mostly 2 cells wide, never producing underleaves (18:2). Gemmae angular-stellate, (14:6; 15:4,8; 17:3; 18:5), produced in all the species.

Perianth unmodified, gradually contracted to the plicate and crenulate to ciliate mouth (17:1). Sporophyte with many rows of cells in seta (14:4). Capsule-wall 3-4-stratose, the inner layer with tangential thickenings and radial thickenings (thus with "bands"), the outer only with radial bands (*i.e.*, with "nodular" thickenings). Dioecious (paroecious in *excisa*).

The subgenus *Dilophozia* has been very variously treated. The present circumscription agrees most closely with that of Müller (1939) and Buch (1942), but differs in including also *L. excisa* and *perssonii*. The latter two agree with *Massula* in that the male and female bracts are distinctly dentate (14:8-10), and in the paroecious inflorescence (of *excisa*), as well as in their general features. However, their oil-bodies are as close or closer to those of *Dilophozia* (compare 14:2 with 16:3 and 11:8) and their stem-structure is definitely as in *Dilophozia* (compare 14:7 with 17:8 and 12:1). Therefore, they are placed as the Sectio *Excisae* in *Dilophozia*, contrasted to the Sectio *Ventricosae*.

The dorsiventrally differentiated medulla of the stem will separate *Dilophozia* from all other subgenera of *Lophozia*. In that feature the subgenus approaches *Tritomaria*. The dorsiventral differentiation of the medulla is not always equally strongly developed. In *L. ventricosa* (17:8) it is extremely obvious. It is equally well-developed in *L. silvicola* Buch (see Buch, 1933b), and in *L. perssonii* Arnell et Buch (see Buch, 1944). In *L. gracillima*, one of the more erect species, the differentiation is less obvious (and I have not been able to find any well-developed mycorrhizal infections), and the younger portions of the shoots show almost no differentiation (see 15:5,7); (see also Buch, 1933b). However, as a subgeneric character, supplemented by other characteristics, this seems an adequate enough basis for separation.

KEY TO NEARCTIC SPECIES[75]

1. Plants erect or suberect in growth with gemmae-formation (15:1); leaves merely 0.6-0.75 (0.8) as wide as long, rectangular, with narrow lobes (15:9; 16:2); stems with dorsiventral differentiation of medulla slight, only 9-12 (16) cells high at maturity, usually lacking mycorrhizal infestation (15:5,7); perianth at mouth laciniate, the cilia up to 6-8 cells long (16:1). Sectio LONGIDENTATAE ..... 2.

---

74 Only *L. excisa* is unable to produce obvious trigones (14:2,5).

75 Frye and Clark (1945) give no key to the species of *Lophozia* (*Dilophozia*), or to *Massula* (which they do not distinguish from *Dilophozia*). Their "Table of Comparisons" is nearly useless in differentiating the species, since such primary characters as stem-structure are ignored. Their table also contains numerous errors: they attempt to differentiate between species on the basis of whether the androecia are "terminal," "just below the tip," or "farther down the shoot." Any experienced worker is well aware of the fact

2. Gemmae reddish-brown at maturity (even in diffuse light); oil-bodies obviously composed of numerous, somewhat protuberant oil-globules (16:3) .....*L. longidens.*

2. Gemmae yellowish-green to yellowish (even in intense light) (15:4,8); oil-bodies composed of difficultly perceptible oil-globules, appearing nearly smooth ..... *L. gracillima.*[76]

1. Plants decumbent in growth, the gemmiparous shoot-apices merely ascending; leaves 0.75-1.25 as wide as long, ovate-rectangular to quadrate or orbicular (16:4,6-7; 17:5; 18:2-4), with broad obtuse or triangular lobes; stems 16-22 cells high usually, with strong dorsiventral differentiation of medulla (14:7; 17:8); perianth-mouth crenulate or with teeth 1-4 cells long (14:1; 17:7) ..... 3.

3. Paroecious; gemmae purplish; male and female bracts distinctly dentate (14:8-10); perianth-mouth with lobes crenulate by projecting cells (14:1); plants fleshy, only 5-10 mm long. Sectio EXCISAE[77] ..... 4.

4. Leaves orbicular, bilobed 1/5-1/4 (14:3,11), on normal leaves never with antical teeth or small lobes; underleaves absent on sterile shoots; usually with gemmae (14:6) .....*L. excisa.*

---

that the position of the *androecia* is a temporally and not genetically controlled factor. Again, they attempt a separation on gemmae color: a genetically controlled feature. However, they indicate variation of from yellow to greenish to reddish-brown for both *L. confertifolia* (a synonym, *fide* Buch of *wenzelii*) and *L. longidens*. However, the presence of pigments of the walls (reddish to brownish) distinguishes *longidens*. They are apparently confusing elements belonging to the distinct *L. gracillima*, which has greenish gemmae, with *L. longidens*, which always has reddish-brown gemmae. Under *porphyroleuca* they give the gemmae as yellow-green to yellow-brown in color; they are always yellowish-green; the leaves of *porphyroleuca* are given as equal in width and length: one of the most reliable differential characters of *porphyroleuca* are the narrow leaves, 0.75-0.95 as wide as long. Similarly, the pigmentation or lack of pigmentation of the rhizoid-bases is meaningless as a differential character (in *Dilophozia*); they give the rhizoids of *L. porphyroleuca* as colorless whereas in my experience they are often reddish at base. Exposed material of other species undergoes probably similar variation. They also attempt to separate between species on the basis of size of the trigones, apparently quite overlooking the work of Buch (1933a) who demonstrated that in *Dilophozia* the trigone size is essentially a factor of the transpiration coefficient and not a genetic factor. Therefore, when they separate *ventricosa* with "small" trigones from *porphyroleuca* with "bulging" trigones they largely perpetuate an illusion. It is apparent, therefore, that many if not most of the differences given in their table represent either temporally or ecologically-controlled (hence phenotypic) differences. This predominance of non-genetic differences cited completely obscures the few valid genotypically controlled characteristics that serve to separate the difficult species of this subgenus: such as the type of growth, gemmae-color, etc.

76 This species has not been previously reported from North America. It is apparently quite discrete from *L. longidens* in gemmae color and size, in the more yellowish color of the entire plant (vs. a deeper green color in *longidens*), in the less distinctly papillose oil-bodies, and in the smaller, smoother spores. Frye and Clark (1945) in their "Table of Comparisons" and their description of *L. longidens* appear to confuse it with *longidens*, but do not mention *gracillima* in the synonymy of *longidens*. They state the gemmae are greenish to reddish-brown in *longidens*—a variation which Buch (1934) has expressly indicated as never occurring. In my limited experience with the species I find that Buch's statements are founded upon fact, and the species is now universally accepted in Europe. I have collected the species twice: MINNESOTA. Cook Co.: on decaying shaded moist log on Pigeon Point. MICHIGAN. Keweenaw Co: Amygdaloid Island, near Isle Royale.

77 The European *L. perssonii* Arnell et Buch is the only other species, to my knowledge, that belongs in the Sectio *Excisae;* it differs in the reddish-brown gemmae, the dioecious inflorescence, the calcicolous habitat, and the shortly ciliate perianth-mouth. (The latter also separates it from the *alpestris-latifolia* complex, to which the gemmae-color would ally it.)

4. Leaves broad-ovate, bilobed 1/3-1/2, on many normal leaves with the antical or both antical and postical teeth; underleaves present on sterile shoots; gemmae unknown ..... *L. elongata.*[78]

3. Dioecious; gemmae yellowish-green to reddish-brown; both male and female bracts with lobes entire (17:1-2,6); perianth-mouth generally with at least scattered teeth 1-2 or more cells long (17:7); plants mostly 1-4 cm. long, often brownish or reddish pigmented. Sectio VENTRICOSAE ..... 5.

5. Gemmae reddish-brown or purplish (18:5-6,15); leaves on well-developed shoots as wide or wider than long (18:7-8,12-13); leaf-cells often with walls more or less brownish ..... 6.

6. Cells of leaf-apices 18-20 μ, of leaf-middle 20 x 25 μ; leaves varying from 0.9-1.05 as wide as long (18:1-4); gemmae red-brown, 16-20 x 16-24 μ (18:5); leaves bilobed about 1/5-1/4, the sinus crescentic to rectangular (18:2-4); perianth-mouth with occasional 1-celled teeth; spores 12-14 μ ..... *L. alpestris.*

6. Cells of leaf-apices 24-28 (30) μ (18:10), of leaf-middle 24-28 x 28-36 μ; leaves varying from 1.1-1.5 as wide as long, transversely rectangular, bilobed 1/4-1/2, the sinus rectangular to acute (18:11-13); gemmae 22-32 (a few to 36-38) μ long (18:15); perianth-mouth evenly crenulate by projecting cell-tips (18:9); spores 14.5-18 μ ..... *L. latifolia* sp. n.*

5. Gemmae greenish to nearly colorless; leaves on well-developed shoots from subequally long and wide to longer than wide (or leaves strongly concave); leaf-cells with walls colorless (rarely reddish in plants with strongly bulging trigones) ..... 7.

7. Leaves strongly concave, saucer-shaped, 1.00-1.2 as wide as long, divided 1/6-1/4 by a crescentic or obtuse, shallow sinus; perianth-mouth denticulate with 1-celled teeth; cells 22-25 μ in leaf-lobes, 20-25 x 30 μ in leaf-middle. Arctic-alpine ..... *L. wenzelii.*[79]

7. Leaves flat or scarcely concave, not with distinctly incurved lobes, 0.7-1.05 as wide as long, divided 1/4-1/3 by an obtuse to rectangular (rarely crescentic) sinus; perianth-mouth with some of the teeth usually 2-3-celled; cells of leaf-lobes 16-22 or 25 μ ..... 8.

8. Perianth-mouth with teeth many 2-4 cells long; leaves narrow, 0.75-0.95 as wide as long, even on plants from insolated sites; cells normally strongly collenchymatous, with very large bulging trigones; oil-bodies 8-10 per cell. (Only on decaying logs and peat) ..... *L. porphyroleuca.*

8. Perianth-mouth with teeth only 1-2 cells long; cells usually moderately collenchymatous, (16:5,8; 17:4) trigones usually varying from little to not bulging; oil-bodies 10-25 per cell ..... 9.

9. Leaves 0.75-0.95 as wide as long, even in densely insolated sites, pale green (16:4-7); oil-bodies circular or nearly, 15-25 per cell (16:5,8-9), each consisting of a large inner highly refractive sphere surrounded by a mantle of obscure, smaller spherules ..... *L. silvicola.*

---

78 Upon the authority of Evans, the species is placed in *Orthocaulis*, in the Buch, Evans, Verdoorn list (1938). The frequent occurrence of underleaves, even on sterile shoots, perhaps justified placing the species there. It has been traditional to place it in the Sectio *Excisae*, however, as in Müller (1910) and Buch (1933). Frye and Clark follow Evans, but clearly indicate their doubts regarding the position of the species in *Orthocaulis*. I tentatively key it out in both subgenera, since I have not seen material of it, and cannot judge in which subgenus it should be placed (without examining stem-cross sections, which should definitely decide the case).

* Description appearing simultaneously elsewhere.

79 *L. confertifolia*, which is now generally accepted as a synonym of *L. wenzelii* is stated to have the gemmae from greenish to reddish in color.

9. Leaves 0.95-1.05 as wide as long (17:5) (except plants from densely shaded areas), deeper green (sometimes reddish-tinged); oil-bodies more or less ovoid, 10-15 per cell, larger (17:4), each consisting of a large number of smaller spherules (without a larger sphere within, in all but exceptional cases) ..... 10.
10. Plants small, 1-2.5 cm, rarely reddish-tinged; perianths less than 1 x 3 mm in size ..... *L. ventricosa* (typical)
10. Plants larger, 2.5-6 cm long, the perianths 1 x 3 mm or larger, longly exserted, carmine pigmented (17:1) ..... *L. ventricosa* var. *longiflora*.

As is indicated in the above key, the restricted subgenus *Dilophozia* is here divided into what I consider to be three sharply definable species groups or sections. These three sections are of interest in that they appear, superficially at least, to show diverse relationships. The Sectio *Longidentae* appears to connect *Lophozia* with *Tritomaria*: it has the leaves dorsally often nearly transversely inserted (15:1). It also has a leaf-shape somewhat reminiscent of *Tritomaria* (especially *scitula*) (compare 15:9 and 16:2 with 22:10, 12 and 23:7). The longly ciliate-dentate perianth mouth also is reminiscent of *Tritomaria* (compare 16:1 with 23:10).

The Sectio *Excisae* appears to connect *Lophozia* with *Isopaches*: the two groups sharing similarly dentate perigonal and perichaetial bracts, (compare 14:8-10 with 13:2), a similar leaf-shape and leaf-insertion (compare 14:3,11 with 13:7), and inability to develop large trigones (compare 14:2 and 5 with 13:3-4). The thick, fleshy stems of the two groups, and small size as well as similarity in facies seem suggestive, but may be due to convergence.

The Sectio *Ventricosae*, of the three sections, appears to occupy the most isolated position. Through *L. alpestris* it may be connected to the Sectio *Excisae*: but it has no apparent relatives in any other genus or subgenus.

The three sections may be briefly reviewed as follows:

Sectio Longidentae.—This section, including only *L. longidens* and *gracillima* differs from other sections in the narrow leaves with drawn-out, narrow lobes (15:9, 16:2); the relatively subtransverse line of insertion of the dorsal portions of the leaves (15:1); the very obviously ascending to suberect gemmiparous shoots; the smaller stems, that are nearly free of mycorrhizal infection and only 9-12 cells high at maturity (15:7), with relatively slight dorsiventral differentiation of the medulla; in the longly ciliate-dentate perianth-mouth lobes (16:1); and in the more or less obviously dentate perichaetial bracts.

Sectio Excisae.—As previously stressed, the Sectio *Excisae* is here considered as a member of the subgenus *Dilophozia* (from which it might, however, conceivably be subgenerically separated). It is much more distinctly related to *Dilophozia* than to *Massula* (in which K. Müller, 1939, and Buch, 1942, placed it). The primary characters that serve to place it in *Dilophozia* are:

11. The oil-bodies. In *excisa* these are mostly 6-8 per cell and 5-7 μ to 5 x 9 μ; in *perssonii* they are 3-8 per cell and 4-8 μ x 4 x 9 μ. They are, therefore, con-

siderably larger than usual for *Massula*, and occur many fewer per cell. Furthermore, they appear to be composed very distinctly of fine oil-spherules (at least in *excisa*, much as in *Dilophozia*, and are not as highly refractive nor as homogeneous in appearance as in *Massula*.

2. The leaf-cells. These are rather distinctly collenchymatous in *perssonii* (see Buch, 1944, p. 383, figs. 5a-b) and slightly collenchymatous in *excisa*.
3. The stem-structure. In both species the medulla is not homogeneous. The ventral two-thirds (and often the ventral ¾) of the medulla is attacked by mycorrhiza, rendering the lower half or more of the medulla spongy, and brownish, with only isolated cells remaining undestroyed by mycorrhiza. I have studied the stem-section of *excisa* (14:7) and find it to be identical with that of *perssonii*. In both of these species the medullary cells are not very highly differentiated in size, the ventral being little smaller, but the medulla is characterized by the fact that so much of it is destroyed by mycorrhizal activity (more than in *Tritomaria* or *Saccobasis*, compare 14:7 and 17:8; 24:5). In the stem-structure, therefore, the Sectio *Excisae* very closely approaches *Dilophozia*, and is obviously different from *Massula* (compare 10:9).
4. The leaves are not distinctly wider than long. This is as in *Dilophozia*, but unlike *Massula*, in which the leaves are usually lax and characteristically wider than long.

The differences from the other two sections of *Dilophozia* are as follows:

1. Plants smaller (only to 1 cm), with thicker, fleshier stems.
2. Stems with mycorrhizal tissue occupying more than two-thirds of the height of the medulla, but with relatively little differentiation in size of cells.
3. Leaves somewhat less obliquely inserted (angle between stem-axis and line of insertion of leaves 60-80°: *i.e.*, approaching subtransverse). In the *Ventricosae* it is generally 30-45°.
4. Inflorescence paroecious or dioecious.
5. Female bracts more or less strongly dentate on lobes.
6. Leaf-cells thin-walled and able to produce only minute to straight-sided (not bulging) trigones.
7. Leaves as wide as long, round-quadrate, 1/4-1/3 bilobed.
8. Spores relatively large, mostly 14-18 μ.

Sectio Ventricosae.—This section includes species with relatively obliquely inserted leaves (at an angle of about 30-45°) (18:4) that have rather broad, often obtuse or rectangular lobes (16:4,6-7; 17:5; 18:2-4); the decumbent to slightly ascending growth (even of gemmiparous shoots); in the higher stems (mostly 16-22 cells high) (17:8), with strong dorsiventral differentiation of the medulla; in the shortly dentate or merely crenulate perianth-mouth (17:7), with the teeth merely 1-3, rarely 4, cells long; and in the entire lobes of the perichaetical and perigonal bracts (17:1-2, 6).

TRITOMARIA Schiffn. emend. Buch.

(Plates 22-24)

I follow Buch (1933) in his circumspection of *Tritomaria*.[80] The genus as restricted exhibits distinct relationships with *Saccobasis* (see p. 66) and with *Dilophozia* (see p. 61), but not with other groups.

---

80 It may conceivably be more desirable to include *Saccobasis* in *Tritomaria* as a subgenus. See discussion on p. 67. Joergensen (1934) also has previously placed it in *Tritomaria*.

The genus, as delimited here, may be defined briefly as follows:

Gametophyte growing rather decumbent (*scitula* and *quinquedentata*) or sometimes strongly ascending (*exsecta, exsectiformis*) but always with the shoot apices strongly autonomously acroscopically curved (22:7). Stem mostly 12-16 cell-layers high (22:1; 24:5), with the cortical cells distinctly elongate (2.5-3 times as long as wide) (22:2) slightly to distinctly narrower than the basal leaf-cells (22:3); medulla with a distinct dorsiventral differentiation into a dorsal region of large, elongate, hyaline cells, and a ventral region of much smaller, shorter, compact cells (22:1; 24:5); the small ventral medullary cells in large part attacked and destroyed by mycorrhiza, becoming brownish (the stems, in ventral aspect, therefore always deeply pigmented, even when the dorsal side is green). Ventral row of stem-sectors obsolete, at most 2 cells wide (24:2), not developing underleaves. Rhizoids numerous, in a dense ventral mat (24:1). Leaves generally trilobed: originating from an originally bilobed leaf (22:12) in which the ventral lobe is considerably larger than the dorsal, with the ventral leaf-margin longer, more strongly arched, as in *Dilophozia* (compare 22:12 and 15:9); leaves more or less asymmetric (23:7; 24:6) the ventral margin usually longer than the dorsal (little longer in *scitula*, 22:10); leaf-insertion basically oblique on ventral two-thirds (22:4; 24:1), becoming virtually or quite transverse on dorsal third (22:8), the plane of the leaf never horizontally spreading but essentially in a plane with the transverse section of the stem (i.e., leaf-plane at right angles to axis); with the dorsally transverse insertion, the leaves become slightly dorsally secund (as in *Anastrophyllum*), especially in drying. Leaf cells always distinctly collenchymatous: able to develop large and bulging, sometimes confluent trigones (22:3; 24:3-4) moderate in size (width 8-20 μ), but often becoming notably elongate (unlike in *Dilophozia*) and 36-48 (56) μ long and rectangular (22:3); cuticle able to develop distinct papillae (which in the region of cell-elongation become delicate rugae); oil-bodies as in *Dilophozia*, moderate in size (4-8 μ), consisting of numerous distinct globules, hence appearing coarsely granulose or papillose, and moderate in number (5-12 per cell, but up to 20 or more per cell in the elongate cells) (22:11). Gemmae produced in all species, rare in *quinquedentata* (22:7,9; 23:3,6).

Perianth large, distally plicate, with a distinct dorsal fold (23:5), dentate at mouth (23:10), unspecialized; bracts 3-4 (5) lobed, lobes entire, usually asymmetric and like leaves (23:11); bracteole absent. Androecia with bracts saccate, each usually with two antheridia in axil; antheridia with stalk uniseriate (*exsecta*) or largely uniseriate with occasional cells divided by vertical walls (*scitula*) (22:5-6) or uniformly biseriate (*quinquedentata*). Capsule-wall 3-stratose (*exsecta, exsectiformis*) to 5-stratose (*quinquedentata*), the inner walls with annular bands of thickening (23:1), the outer wall with them uniformly nodular (*i.e.*, confined to radial walls) (23:2); seta of numerous rows of cells, of unspecialized type.

Saccobasis polita agrees with most of the above diagnosis. The chief differences cited by Meylan (1924) and Buch (1933) are in the leaf-insertion

and relative length of the cortical stem-cells. The first is a valid characteristic, and serves to separate *Saccobasis* not only from *Tritomaria* but from other Lophoziaceae as well. As is shown under *Lophozia* subg. *Massula*, the length of the cortical stem-cells (and their width relative to the basal leaf-cells), is apt to vary very widely among otherwise closely related species. I am therefore not willing to concede this as a generic character.[81] The other difference cited by Buch (1933) lies in the subequally 3-lobed leaves. If 25:6-7 are compared with 22:10 (upper leaf) it will be seen that this difference is also relatively slight (see further discussion, p. 67). The subequally trilobed leaves occur again in *T. scitula*, and from a *scitula*-like common ancestral form it appears possible to derive all of the species of the genus, as well as *Saccobasis*. Such an ancestral form very closely approaches *Lophozia*, subgenus *Dilophozia* (as previously stressed), in the following characters: a. Tendency for development of 3-lobed leaves on strong shoots. b. Ventral half of leaf obliquely inserted, dorsal less obliquely inserted. c. Stem with a ventral mycorrhizal tissue of small cells in the medulla. d. Perianth unmodified.

In *Tritomaria scitula* the concave-canaliculate leaf-form so characteristic of *T. exsecta* and *exsectiformis* is less developed (22:7). It is also scarcely evident in the spreading-leaved forms of *T. quinquedentata*.

The genus, as here restricted, is related very closely to *Dilophozia* K. M., and differs from it in that the 3-lobed character of the leaves is fixed (in *Dilophozia* only incidental and usually confined to robust shoots), and in that the leaves become more nearly transversely inserted (but compare here *L. gracillima*, 15:1, and *Tritomaria quinquedentata*, 24:1, 7, in which there is virtually no difference). In fact, I am totally unable to see a really significant break in the following series, as regards leaf-insertion: *Lophozia gracillima* and *longidens* → *Tritomaria quinquedentata* → *Tritomaria exsecta*.

It is obvious, therefore, that *Tritomaria* as a genus is very poorly separable from *Lophozia*: the only reason for retaining it as a genus is the fact that it includes, itself, two distinctive elements that may well be considered subgenerically distinct. The oil-body structure is virtually identical, as well as the size and number of oil-bodies per cell, as in *Dilophozia*, and so are the perianth, collenchymatous nature of the leaf-cells, etc. The cuticle in *Tritomaria* is, however, usually distinctly papillose, but smooth or nearly in *Dilophozia*.

Buch (1933) first placed *Jungermania quinquedentata* into *Tritomaria*, largely on the basis of the leaf-shape, absence of under-leaves, stem-structure, and the more or less transverse insertion of the dorsal half of the leaf. Previously it had been placed in *Barbilophozia*, and Meylan (1939) believed it might well have been left there. I would definitely agree with Buch that it falls much nearer to *Tritomaria*. However, as Müller (1948) points out, *T. quinquedentata* differs in several rather fundamental features from *Tritomaria* (s. str., *Eutritomaria* of this paper): it has a biseriate antheridial stalk

81 The relatively thicker walls of the cortical cells of *Saccobasis* also are scarcely a valid criterion. If my figures 22:2 and 25:9 are compared it will be seen there is virtually no difference between the two genera in thickness of the cortical stem cells.

and a 5-stratose capsule-wall. In the latter it differs also from *Barbilophozia*. Since, in addition, the nearly horizontal manner of growth, as well as the less transversely inserted dorsal half of the leaf, give the species a very different facies, I believe it to be best to exclude it from the *scitula-exsecta* complex as a separate subgenus, or section. The differences from *Eutritomaria* are contrasted in the following key.[82]

KEY TO NEARCTIC SPECIES (AND SUBGENERA)

1. Leaves distinctly longer than wide, with the ventral sinus varying from narrower than dorsal sinus to absent (22:10; 23:5-7); leaf-cells elongate (except near leaf-margins and apices) (22:3,11); antheridial stalk entirely or largely uniseriate (22:5-6); leaves more or less strongly complicate-canaliculate (22:7-8; 23:5-6); gemmae abundantly present; capsule-wall 3-4-stratose. Subgenus *Eutritomaria* ..... 2.
2. Leaves subequally trilobed, the postical leaf-margin little longer than antical margin (22:7,10); gemmae angulate; cells and gemmae similar to those of *exsectiformis* ..... *T.* (*E.*) *scitula.*
2. Leaves strongly asymmetrically trilobed, the postical margin strongly arched and much longer than antical (23:5-7) ..... 3.
3. Cells of the leaf-middle 8-12 x 10-18 μ, generally with small trigones; cells of margins 8-12 x 10-15 μ; gemmae elliptical, 8-12 x 11-18 μ; perianth-mouth with lobes with numerous, crowded cilia, mostly 1 cell wide to base ..... *T.* (*E.*) *exsecta.*
3. Cells of the leaf-middle 17-22 μ wide x 20-36 μ long, often with bulging trigones; cells of margins 18-20 μ; gemmae angulate (23:3), 14-18 μ x 17-26 μ; perianth-mouth with more distant, scattered cilia, often 2-several cells wide at base (23:10) ..... *T.* (*E.*) *exsectiformis.*

1. Leaves as wide or wider than long, suborbicular when spread out, with the ventral sinus broader than dorsal sinus (24:2,6-7); leaf-cells isodiametric or nearly, except at base of leaf (24:3); antheridial stalk biseriate; leaves with dorsal half often horizontally spreading (24:2,7); gemmae rare, usually absent; capsule-wall 5-stratose. Subgenus *Trilophozia* ..... *T.* (*T.*) *quinquedentata.*

SACCOBASIS Buch

(Plate 25)

The very peculiar form of the leaf-insertion (which does not recur in any other genus of Lophoziaceae) appears to warrant the separation of *Jungermania* (or *Sphenolobus*) *politus* as a discrete genus. Although apparently related most closely to *Tritomaria, Saccobasis* is much more strongly specialized, in the following ways: The leaf-insertion has become extremely specialized, with the line of insertion curving apicad both dorsally and ventrally, but

82 It should be noted, however, that the stalks of the antheridia are rather variable. In *T. quinquedentata* the stalk is apparently uniformly biseriate, in *T. exsecta* uniformly uniseriate. In *T. scitula,* which serves, in some manner, as a common ancestral form, the stalk may be entirely uniseriate (as in *Eutritomaria*) or may have isolated cells divided by transverse partitions (i.e., biseriate), as in *Trilophozia.* This variation recurs again in *T. exsectiformis.* Such variation, within a genus and even within a species, indicates the lack of true phyletic importance of this character, in at least some cases. When Douin (1920) uses such a difference as one of the primary separating characters between the Cephaloziaceae and "Cephaloziellaceae" he is decidedly overevaluating its importance (see also footnote 29).

suddenly curving basal again dorsally and ventrally at the extreme ends of the line of insertion (because of the decurrence of both dorsal and ventral lobes); the ventral leaf-base is especially strongly decurrent. The apical curvature of the dorsal and ventral portions of the line of insertion (excepting the extreme ends) results in an axillary "pocket," such as is not found in other Lophozioid genera. The leaf itself has, secondarily, become equally trilobed (probably from a *T. scitula*-like type of leaf), and the lobes have become relatively short, broad and obtuse. The stem structure is of the *Dilophozia-Tritomaria*-type, i.e., there is dorsiventral differentiation of the medulla, into a ventral band of smaller, shorter, cells,[83] and into a dorsal region of larger, more elongate cells. Like *Tritomaria,* the dorsal cortical cells are elongate, but more so than in that genus, (attaining an average length equal to that of the underlying medullary cells), and they may become extremely pachydermous.[84] Another feature that characterizes *Saccobasis* is the lack of any autonomous dorsal curvature of the stem-apices, as has been stressed by Buch.

It is therefore apparent that *Saccobasis* is very close to *Tritomaria* and shares with it the stem-structure, the elongate, cortical cells, the more or less canaliculate 3-lobed leaves, the relatively narrow cortical cells (averaging narrower than the basal leaf cells),[85] the virtually obsolete ventral stem-sectors that are unable to produce underleaves. It is questionable to me whether to separate the sole species of *Saccobasis* generically from *Tritomaria,* or leave

---

83 Buch (1933) stresses the fact that in *Lophozia* (*Dilophozia*) and *Tritomaria* the ventral medullary band is attacked by mycorrhiza, become brownish and discolored. He, however, apparently did not observe similar mycorrhizal infection in *Saccobasis.* In Norwegian material of *S. polita* I find that the medulla is commonly mycorrhizal ventrally, exactly as in *Dilophozia* and *Tritomaria.* It must be stressed, however, that the dorsiventral differentiation of the medulla is extremely poorly indicated (see 25:8). If one compares L. (*Orthocaulis*) *kunzeanus* and *L.* (*Barbilophozia*) *barbata* stem-sections (1:5 and 8:6) one will easily perceive that the dorsiventral specialization in *Saccobasis* is indicated scarcely more distinctly than in these two subgenera.

84 Buch (1933) figures the cortical extremely pachydermous, with the wall nearly as wide as the lumen. He, however, did not stress the pachydermous nature of the cells as a generic character, obviously because his own experience has shown that the thickness of the cell-wall is largely a reflection of environmental conditions and hence not a genetic character. Frye and Clark (1945, p. 337) separate *Saccobasis* from all other genera of Lophoziaceae, except *Acrobolbus,* because the "cortical cells of the stem with walls about as thick as the diameter of the cell cavity." The utilization of such an environmentally controlled characteristic is of very questionable value. In 25:9 I show the dorsal cortical stem cells of the species, here the walls vary from 1/3-1/6 the thickness of the lumen. Obviously the thickness of the cell-walls must be extremely variable, varying with differences in environmental conditions, and is taxonomically nearly useless for separating genera. It should also be stressed that the length of the cortical cells is scarcely to be considered a valid generic character. In *Lophozia* (*Massula*) *marchica* both dorsal and ventral cortical cells are extremely elongate, yet *L. marchica,* in other characters is related to the other species of *Massula* with shorter and broader cortical cells.

85 Associated with the tendency to produce elongate cortical cells is also a common tendency to produce obviously elongate cells of the leaf-middle and leaf-base—a common feature not found in *Dilophozia.* The leaf-cells often attain a length of 60-100 μ near the leaf-base and become 2.5-5 times as long as wide.

it in *Tritomaria* as a well-isolated subgeneric element. The former seems more reasonable, since the gap between *Tritomaria* and *Saccobasis* is certainly greater than the gap between *Dilophozia* and *Tritomaria*: if we are to consider the latter of generic caliber, the former deserves equal emphasis. Müller (1910, p. 615) has stressed the similarity between the gemmiparous form of *S. polita* and *T. scitula*. He states that this gemmiparous form (called the var. *acuta* Kaal.) "nähert sich sowohl im Habitus wie in der Blattform (gestreckt-dreieckige Lappen) stark dem *S. exsectiformis* var. *aequiloba* [=*T. scitula*] und überbrückt so die anscheinend grosse Kluft zwischen *S. politus* und . . ." *T. scitula*. I have on a previous page stressed the fact that the relatively unspecialized *T. scitula* can serve as a synthetic type from which both *Eutritomaria* and *Trilophozia* as well as the more distantly allied *Saccobasis* can be derived. For that reason it may be desirable to treat *Saccobasis* as a subgenus of *Tritomaria*.

The genus (or subgenus) *Saccobasis* may be formally diagnosed as follows, following largely the original diagnosis by Buch (1933):

Shoots, large, up to 3-5 cm tall, erect or ascending in growth (more rarely decumbent), not distinctly autonomously dorsally curved at the apices. Stem in cross-section about 14-16 cells high, the cortical cells in 1-3 rows more thick-walled than the interior; dorsal cortical cells extremely elongate, more or less thick-walled, 4-8 times as long as wide, somewhat narrower but longer than the basal leaf-cells, as long as the underlying medullary cells; ventral cortical cells short in 1-2 layers, associated with development of rhizoid-initials; medulla consisting of a ventral region of several layers of smaller cells that may become mycorrhizal, occupying circa the basal fourth of the medulla; dorsal portion of medulla of much larger, more hyaline cells, of 2-4 times the length of the ventral medullary cells; ventral stem sectors obsolete, merely 1-2 cell-rows wide, not able to develop underleaves. Rhizoids long and merely moderately numerous (unlike *Tritomaria*). Leaves scarcely succubous, rectangular when spread out and as long as wide to slightly wider than long, erect-spreading, at least on basal half distinctly concave-canaliculate (the apical portions often strongly spreading or reflexed outward and spread out in a plane); leaf nearly equally, shallowly trilobed at the truncate apex, the lobes broad and obtuse, the two ventral lobes apparently originating as in *Tritomaria*. Leaf-insertion essentially forming an inverted catenary curve: both lateral halves of the line of insertion curving towards stem-apex, forming a deep curve open to the stem-apex (resulting in the pocket-like leaf-base); dorsal half of insertion usually reaching further towards the stem apex than the ventral half, at the extreme dorsal end of the insertion barely to slightly decurrent; ventral half of insertion near the ventral end suddenly, strongly curved towards stem-base (in a hook-like manner; the base of the ventral lobe therefore strongly decurrent). Leaf-cells strongly collenchymatous, isodiametric near apices, but near base becoming extremely elongate, somewhat wider than dorsal cortical cells. Gemmae rare, occurring on younger leaves of shoot-apices, angulate, 1-2-celled, rendering the leaves acute-lobed and very similar to those of *T. scitula* in facies.

Dioecious. ♀ bracts in two pairs, somewhat larger than leaves and more deeply lobed. Perianth as in *Tritomaria,* but entire at mouth. ♂ bracts like vegetative leaves, differing only in the somewhat saccate or ventricose bases; antheridia ?1-2 per axil.

Species.—S. polita (Nees) Buch.[86]

ANASTROPHYLLUM (Spr.) St.
(Plates 19-21)

In the critique (p. 25) I have gone into some detail as to the problems of the correct delimitation of this genus. Buch (1933) found the delimitation of the group by Müller (1910) and earlier writers unsatisfactory, and broadened the genus. As Evans (1935) stresses, *Anastrophyllum* as delimited by Buch includes *Sphenolobus*-like forms in which the leaf-insertion is not limited to the acroscopic end of a stem-segment, but extends backward for some distance along the dorsal, lateral boundaries. I find that "*Sphenolobus*" *saxicolus* also has a leaf-insertion of this type, and is more closely related to *Anastrophyllum* than to *Sphenolobus* (s. Buch).

Buch attempted a separation of the elements I include in *Anastrophyllum* into three genera (*Isopaches, Anastrophyllum,* and *Sphenolobus*). There are several good reasons why such a separation cannot be maintained, at least not as given by Buch. The essential distinguishing characters given for these genera by Buch are as follows:

A. Stem small, only about 6-7 cells high; cells non-collenchymatous ..... *Isopaches.*

A. Stem larger, 11 or more cells high; cells collenchymatous (exc. *Sph. minutus*) ..... B.

B. Leaf widest at base, at base extending beyond midline of stem; insertion arched, convex towards the stem-apex, not limited to the acroscopic margin of the segment, but decurrent along the dorsal edge of the lateral edges of the segment ..... *Anastrophyllum.*

B. Leaf widest near middle, at base not extending beyond midline of stem; insertion oblique or oblique on the ventral side of the stem end but transverse for a short distance on the dorsal side of the stem, coinciding with the acroscopic stem-segment margin ..... *Sphenolobus.*

If "*Sphenolobus*" *saxicolus* is compared with "*Anastrophyllum*" *michauxii,*

86 This species appears to have a very restricted range in North America, occurring only in the Arctic-alpine zone and the upper edge of the Subalpine. Frye and Clark (1945) cite it from New Jersey: the only reported station in the United States. This record represents a mistake, as is evident from the synonymy they cite under *Lophozia marchica:* Austin reported *L. marchica* as long ago as 1870, but as *Jungermannia polita,* and this report of *J. polita* Austin nec Nees (= *Lophozia marchica*) appears to be the sole basis for the report of *Saccobasis politus* from the United States.

It has also been reported from Ontario (Cain & Fulford, 1949). I have seen a duplicate of that collection, and find in it only *Marsupella sphacelata* var. *erythrorhiza.* Frye & Clark, in their exsiccati, have issued material supposedly of *Saccobasis;* in the number in the University of Minnesota herbarium I find only *Lophozia* (*O.*) *floerkei.* The only authentic material I have seen of *Saccobasis* from eastern North America is from the east coast of Hudson Bay and the Ungava Bay area (see Schuster, 1950).

it will be seen that the differences cited between the two genera by Buch are quite illusory. The insertion of the leaves of *A. michauxii* is not "bogenformig," as claimed by Buch, but is oblique along virtually the entire lateral portions of the insertion (21:19), becoming very slightly arched only at the ventral point of the insertion, because the ventral margin is slightly arched in insertion and a little decurrent (21:17). As stated by Buch, the dorsal margin follows the lateral edges of the dorsal stem-sectors (*i.e.*, is decurrent along these) (21:18,20). If the figures of *A. michauxii* are compared with those of *"Sphenolobus" saxicolus* a striking similarity will be noted in the leaf insertion, the decurrence along the inner edges of the dorsal lateral margins of the stem-sectors, and in the dilated dorsal leaf-base, which extends nearly or quite across the stem.[87]

It is apparent, therefore, that no real difference exists between the genera *Sphenolobus* and *Anastrophyllum*, as given in Buch (1933, 1942). Similarly, the species *Sph. minutus*, which has a distinctly transverse and non-decurrent dorsal leaf-insertion, appears to be much more closely related to *"Isopaches" hellerianus*. The genus *Sphenolobus* of Buch, although restricted to two species, represents an admixture of phyletically discrete elements, of which one (*minutus*) finds its closest relative with *"Isopaches" hellerianus*, while the other (*saxicolus*) belongs in *Anastrophyllum*, as Buch defines that genus. The sporophyte morphology further confirms such a basic division into two groups (see key), founded on differences in leaf-insertion and cell-structure.

As is previously stressed (p. 25), there is no sharp distinction between the various genera in this complex, and a virtual continuum exists between the more robust species with decurrent dorsal leaf-bases. I therefore prefer to associate all of these types in the single genus *Anastrophyllum*, which may be characterized as follows. In the characterization special emphasis is laid on the differences that separate the genus from *Orthocaulis*.

Gametophyte strongly negatively geotropic in growth, either erect or suberect, especially with formation of gemmiparous shoots (19:7; 20:6; 21:3). Stems 6-16 or more cells high, the cortical layers of cells relatively short, about as wide as the basal leaf cells, merely 1-3 times as long as wide, able to develop thick walls, subequal in size to the medullary cells (or at most slightly smaller) (19:9; 20:8-10; 21:2); medulla nearly or quite homogeneous, at most the ventral 1-3 layers of somewhat smaller cells, not forming a mycorrhizal ventral band. Rhizoids relatively sparse, often nearly none on the terminal erect portions of plants (19:6; 20:6; 21:17). Leaves uniformly bilobed (very occasional leaves with ventral lobe again bilobed, as in upper leaf in 19:1), the sinuses descending ¼-½ the leaf-length normally; leaves always

---

87 When Frye and Clark (1945) give the leaf-insertion of *"Sph." saxicolus* as "transverse" they can scarcely have observed the species. Similarly, they attempt to separate *A. michauxii* "leaves not decurrent") from *A. reichardtii* ("leaves slightly decurrent dorsally"), when the leaves are obviously and distinctly decurrent along the edges of the dorsal margin of the lateral stem-sectors in both species.

more or less complicate, strongly canaliculate or concave (19:1; 20:1-2; 21:6-7,18), the dorsal lobe usually lying over the ventral lobe (except *A. michauxii*). Line of insertion oblique ventrally, dorsally transverse for part or all of its length (20:2-3; 21:6-7), but sometimes with the line of insertion running down along the dorsal lateral boundary of the merophytes, and thus oblique on the innermost end of the line of insertion (19:1,5; 21:18,20). Cells nearly iso-diametric, near the leaf-base becoming merely 1-2 times as long as wide; cuticle usually more or less papillose; oil-bodies moderate in size, mostly 4-9 μ long, relatively few in number (usually 3-9 per cell), distinctly composed of numerous minute oil-spherules, and appearing finally papillose (21:1); cells either collenchymatous or producing equally thickened walls, rather small, mostly 12-18 μ wide (21:1,10; 19:2; 20:8). Ventral stem sectors obsolete, 1-2 cells wide, unable to produce underleaves on sterile stems (19:4; 20:3; 21:17), on fertile stems occasionally producing stalked slime-papillae (21:6). Gemmae, when present, angulate, pigmented (20:5; 21:4,11).

Dioecious. Perianth large, longly exserted beyond bracts, plicate at least on distal third or fourth, never beaked, typically with a distinct dorsal furrow, often extending to near base (19:7; 20:1; 21:8), either terete or somewhat dorsiventrally flattened. Perichaetial bracts variable: sometimes simply bilobed and like leaves, sometimes 3-4-lobed (20:1), sometimes with lobes dentate (19:8), always free from each other and from perianth. Sporophyte with seta of numerous cell-rows or, in reduced species, merely of 4 inner and 8 outer rows of cells. Capsule varying from 2-4-stratose or even 5-stratose, the inner layer with annular, the outer with nodular thickenings.

The genus, as delimited, is sharply discrete from all groups except the subgenus *Orthocaulis* of *Lophozia,* from near which (as Buch clearly perceived), it is descended. *Orthocaulis* is also characterized by a strongly negatively geotropic growth of the shoot-apex; it has the leaves suggestively similar, and with similarly small cells; it has a uniform medulla like *Anastrophyllum,* and, suggestively, has the subtransverse leaf-insertion which may have easily been ancestral to the existing condition in *Anastrophyllum.* The presence of relatively few, moderate-sized oil-bodies (mostly 4-9 per cell in each group), is also suggestive (compare 2:7 with 21:1,10). At the same time, it has not acquired the specializations of the latter: it retains wide ventral stem sectors, and, in several species, ciliate postical leaf-bases — characters which I consider definitely archaic in the group. The similarities between *Orthocaulis* and *Anastrophyllum* are of the nature of sharing of what appear to be primitive characteristics, and the contrasting differences between them appear fundamental enough to warrant generic segregation.

The genus as above delimited is somewhat polymorphic, including four small monotypic subgenera, and a large, polytypic subgenus (*Euanastrophyllum*). These groups are all represented in North America, except for the subgenus *Eremonotus*. The five subgenera belong to two distinct types, which conceivably may be considered generically distinct. These may be separated by the key on p. 35.

THE EURYLOBUS-EUANASTROPHYLLUM COMPLEX

The two subgenera placed here have in common a number of features (in addition to those mentioned on the generic diagnosis), as follows: Gametophyte unreduced, robust (mostly 1.5-3 mm or more wide), lacking any dimorphism between gemmiparous and non-gemmiparous shoots. Stems 12-16 or more cells high (19:9). Leaves on well-developed shoots with the dorsal and ventral bases more or less dilated, often somewhat cordate when spread out (19:3; 21:13); line of insertion slightly arcuate, with the convexity directed towards the stem-apex, not restricted to the acroscopic end of the merophyte, extending backward (i.e., decurrent) for a short distance at least dorsally, and usually ventrally along the lateral boundaries of the segment (19:1,4,5; 21:17-20); the dorsal end of the line of insertion thus not strictly transverse, but appearing oblique at least at the innermost edge. Leaf-bases dilated dorsally, and usually ventrally and arching across stem, generally notably so (19:1,4-5; 21:18,20). Cells distinctly (19:2) to strongly (21:10) collenchymatous, with thin-walls. Perianth terete, never at all dorsiventrally flattened. Sporophyte with seta of numerous cell-rows. Capsule-wall 3 5-stratose.

The two included subgenera may be individually treated as follows:

Subgenus 1. **Eurylobus** subg. nov.

This subgenus is established for the single, isolated species, *"Sphenolobus" saxicolus*. As has been stressed, this has very little in common with *Sphenolobus minutus* (the other species of *Sphenolobus* of recent workers). The subgenus is somewhat intermediate, and occupies a synthetic position. In the occasional trilobed leaves (19:1), the cell-net, the shortness and broadness of the leaves and lobes, it recalls such species as *Lophozia* (*Orthocaulis*) *atlanticus* and *kunzeanus* (with which it shares a somewhat similar leaf insertion; compare, for instance 19:6 with 3:1). In the fact that the leaves are not clearly widest at base (19:3,8) it differs from *Euanastrophyllum* (21:13) and approaches *Sphenolobus* (20:4,11). It also has the leaves less decurrent dorsally than *Euanastrophyllum* (19:1, lower leaf), and in that manner again approaches *Sphenolobus*. The leaf-cells are also only moderately collenchymatous (but occasionally have much larger trigones than in 19:2), and are more or less intermediate between the non-collenchymatous ones of the *Sphenolobus-Crossocalyx-Eremonotus* complex and the strongly collenchymatous ones of *Euanastrophyllum*.

The subgenus may be briefly characterized as follows: Leaves much wider than long, widest beyond middle, the lobes more or less dilated, broad (19:3,8); sinus descending half or more the leaf-length: leaves little secund, strongly concave-cupped, with incurved lobes. Cells thin-walled with moderate-sized trigones (19:2). Gemmae absent.

Species.—Anastrophyllum (*Eurylobus*) *saxicolus* (Schrad.) comb. n.[88]

88 This species has not been previously reported from the United States. I have collected it a single time, at Pigeon Point, Cook Co., Minnesota, Sept. 2, 1947, *Schuster 5008*.

Subgenus 2. EUANASTROPHYLLUM Schuster, 1949

This subgenus corresponds exactly with the genus *Anastrophyllum* as in Buch (1933), Evans (1935), etc. The group includes a large series of species that have a strong similarity, as regards facies. The species almost all have strongly secund, boat-shaped, canaliculate leaves, very often extremely elongate and gradually narrowed from a broad, dilated base. Our common species of the subgenus (*A. michauxii*) shows this to a lesser degree, has unusually short leaves (21:13), and is further aberrant in that the dorsal lobe of the leaf is usually erect or squarrose (21:20), never lying over the ventral lobe as in the other species. This species differs further in the clavate perianth, widest distally, which almost lacks plicae, except for the distal fourth or fifth, and in the strongly spreading perichaetial bracts that are scarcely modified from the vegetative leaves. For that reason further study may make it desirable to separate out this anomalous species as a separate subgenus. Including *A. michauxii*, the subgenus may be separated by the following diagnosis:

Leaves as wide or usually longer than wide, often conspicuously so, clearly widest just above the base, the lobes narrow (21:13), sinus descending ¼-1/3 (rarely ½) the leaf-length, often less; leaves strongly secund, especially when dry, canaliculate-complicate. Cells thin-walled and with large, often confluent, usually brownish trigones (21:10).

Nearctic species.—*Anastrophyllum michauxii* (Web.) Buch and *A. reichardtii* (Juratz.) Steph.; these may be separated by the following key.

KEY TO NEARCTIC SPECIES

1. Leaves about as wide as long or slightly wider, nearly equally (1/3-1/2) bilobed, the dorsal lobe erect, squarrose, spreading from stem; perianth obpyriform to clavate, widest above middle; bracts strongly spreading away from perianth at base; gemmae frequent; plants to 1.5-3 mm wide ..... *A. michauxii.*

1. Leaves distinctly longer than wide, the ventral half distinctly larger than dorsal, the dorsal half not erect, 1/4-1/3 bilobed, lying over stem, the leaves thus strongly complicate and canaliculate-concave; perianth widest in basal half, ovoid, gradually narrowed in distal half; bracts more or less erect and sheathing base of perianth; gemmae absent; plants 1-1.5 mm wide ..... *A. reichardtii.*[89]

THE SPHENOLOBUS-CROSSOCALYX-EREMONOTUS COMPLEX

The three included subgenera (most recently all separated generically) have in common the following basic features: Gametophyte reduced, small (mostly 0.4-1.0 mm wide), with distinct dimorphism between non-gemmiparous shoots with spreading leaves (20:2-3, 21:6-7) and gemmiparous shoots with more erect to appressed, reduced leaves (20:6, 21:3); or gemmae absent. Stems 6-11 cells high (20:10, 21:2). Leaves not with dilated bases, not clasping or

---

89 Frye and Clark use as a separating character the lack of decurrence of the leaves in *michauxii*, vs. the slight dorsal decurrence of the leaves in *reichardtii*. However, both species have a distinctly decurrent antical leaf-base, and this characteristic is one of the most important subgeneric characters of *Euanastrophyllum*.

clasping-sheathing the stems, never cordate when flattened out (20:4-11; 21:5), widest usually near middle; line of insertion oblique ventrally, transverse dorsally (20:2-3; 21:6-7), restricted strictly to acroscopic end of segment, and not at all decurrent either dorsally or ventrally; leaf-bases not at all arching beyond midline of stem dorsally (20:2; 21:7) on normal leaves of sterile shoots, or ventrally (20:3; 21.6). Cells not collenchymatous, with small or no trigones, but with the ability to develop strong, and equally thickened walls (20:8; 21:1). Perianths slightly to distinct dorsiventrally flattened, at least above (21:8). Capsule wall bistratose.

Müller (1947) first suggested that *Crossocalyx* and *Eremonotus* might "better have been left as subgenera of *Sphenolobus*." I agree in that the three groups are very closely related, but cannot agree with Müller in retaining *Sphenolobus* as the generic name. For reasons of priority, the generic name *Eremonotus* predates *Sphenolobus* by two years as a generic entity (see p. 27). Therefore I would use *Eremonotus* Ldb. and Kaal. for this same entity, should the included subgenera be preferably separated as a genus.

The three subgenera I here unite in one complex agree in possessing a certain number of critical features that set it off from the nearest related complexes (*Anastrophyllum, Orthocaulis*), among them:

a. The capsule-wall is bistratose (rather than 3-4 stratose).

b. The leaf-cells are able to produce equally thickened walls.

c. The leaf-form and leaf-insertion are identical in all three groups: oblique along the ventral half or two-thirds, and distinctly transverse along the dorsal portion of the line of insertion, with the dorsal leaf-bases not expanded (hence not extending beyond the stem-midline), and not at all decurrent.

d. The perianth has a distinct dorsal, deep, broad fold, extending nearly to base (at least in the period before maturation of the sporophyte), and tends to be transverse in section.[90]

e. The stem-structure is essentially the same: consisting of 1-2 or 3 cortical layers of thick-walled cells that are only about 1.2-2.0 as long as wide, and a varying number of rows of medullary cells that are not conspicuously larger in cross-section, but are more elongate; the ventral medullary region is furthermore not regularly attacked by mycorrhiza, though the cortical 1-2 ventral layers (and sometimes the lateral and dorsal cortical cells) are attacked in age. Unlike the related *Euanastrophyllum*, the stem is smaller: merely 5-11 cells high.

f. Very distinctly complicate-bilobed leaves, inserted somewhat pectinately, spreading laterally.

g. Erect or strongly ascending growth with gemmae production, with the gemmiparous leaves reduced, denticulate, erect to appressed (resulting in filiform gemmiparous shoots). In *Eremonotus* gemmae are unknown, however.

Only *Sphenolobus* and *Crossocalyx* occur in North America, hence *Eremonotus* will not be further treated here.

---

90 This is scarcely distinct in *A. minutus*, but is obvious in *hellerianus*, while it becomes marked in the subgenus *Eremonotus*, in which the perianth is strongly flattened.

Subgenus 3. SPHENOLOBUS Lindb., emend. R. M. S.

In addition to the characters that *Sphenolobus* shares in common with the subgenera *Crossocalyx* and *Eremonotus* (given above), it differs in the following characteristics:

Gametophyte moderately small, 0.8-1.2, rarely 1.5 mm wide. Stem about 10-11 cells high (20:10). Gemmiparous plants erect, more or less reduced, slender, filiform, (especially under xeric conditions), with erect reduced leaves (20:6); gemmae mostly 2-celled, a few 3-4 celled (20:5). Perichaetial bracts irregularly 2-4-lobed, the lobes entire-margined. Perianth not or scarcely dorsiventrally compressed. Sporophyte with seta of many cell-rows. Capsule-wall tending to have both inner and outer layers with semiannular thickenings (fide Frye & Clark, 1945, p. 377).

The subgenus *Sphenolobus* is here restricted to the single species *A.* (*Sphenolobus*) *minutus* (Cr.) Schuster.

The single included species is very closely related to *Crossocalyx*, and differs from it in my estimate only in the degree of reduction that has occurred in the number of rows of cells that constitute the axis of gametophyte and sporophyte: the less reduced *A. minutus* has the stem 10-11 cells high, and the seta of the sporophyte essentially of 3 tiers of cells, the outer with over 12 rows of cells. Furthermore, the gemmae remain mostly 2-celled (a few may even be 3-4-celled; see 20:5). Müller (1947) stressed that *Crossocalyx* was closely related to *Eremonotus*, in part because of the presence of a distinct dorsal groove of the perianth (21:8); such a dorsal sulcus also occurs in *A. minutus* (20:1). The leaves of *A. minutus* are always obviously unequally bilobed, the ventral lobe being distinctly larger (20:2-4, 11); in *A. hellerianus* the leaf-lobes have become nearly or quite equal in size (21:5-7).

Subgenus 4. CROSSOCALYX (Meyl.) Schuster

Gametophyte minute, 0.5-0.85 mm wide. Stem only 6-7 cells high (21:2). Plants usually with gametophyte extremely dimorphic, the vegetative shoots with large, spreading complicate leaves (21:6-7), the gemmiparous shoots erect, with reduced, more or less imbricate leaves (21:3, here less obviously developed, the plant coming from an unusually moist site); gemmae when occurring on filiform shoots 1-celled, quadrangular (21:4), when occurring on normal leaves mostly 2-celled. Perichaetial bracts bilobed like leaves, but margins more or less spinous-dentate (at least on robust plants); leaves below bracts tending to develop basal spinous teeth (21:7). Perianth, at least before maturity of sporophytes, more or less dorsally compressed above (21:8), with dorsal sulcus usually obvious but with lateral and ventral sulci obsolete. Sporophyte with seta of two tiers of cells, the inner of four rows, the outer of 8 rows of cells. Capsule-wall bistratose.

Species.—Anastrophyllum (*Crossocalyx*) *hellerianus* (Nees) Schuster.

The sole species has had a checkered history, having been placed in the following genera during the last century: *Jungermania, Diplophyllum, Diplo-*

phylleia, Cephalozia, Prionolobus, Sphenolobus, Cephalozia, Isopaches, Crossocalyx, and now *Anastrophyllum.* Should a more radical division of *Anastrophyllum* (s. lat.) be feasible, the species would go into the genus *Eremonotus* (see p. 27).

TEMNOMA Mitt.

(Plate 4)

The genus *Temnoma* (as typified by *T. setiforme*) occupies a relatively isolated position.[91] In the erect or ascending mode of growth, the nearly transversely inserted leaves, and the large underleaves, as well as the stem-structure, leaf-cells, etc., it approaches *Orthocaulis* Buch, through *L.* (*Orthocaulis*) *quadrilobus.* Buch first demonstrated the existence of such a relationship, and removed the genus from the old portmanteau family Ptilidiaceae.

The genus, unlike *Orthocaulis,* has retained somewhat larger underleaves (ventral stem-sectors about ¼ the width of the circumference), which have retained the deeply bilobed ancestral form. In this feature the genus is more archaic than the other Lophozioid genera and therefore could be placed at the beginning of the system. The leaves, which retain the primitive, nearly transverse insertion have, however, become 4-lobed, and the division of the dorsal and ventral lobes is to be regarded as a secondary feature, or side-wise specialization.[92] As in *Orthocaulis,* the leaf-bases (both dorsal and ventral, of leaves and underleaves) bear cilia or teeth consisting of isodiametric cells. It would seem that the development of such cilia represents a primitive feature recurring again in other primitive genera (*Ptilidiaceae, Trichocoleaceae,* a few species of *Herberta,* such as *hutchinsiae*), and indicates a convergence towards a possibly common ancestral form. Significantly, the ability to develop secondary lobes (as in *Ptilidium*) is very generally correlated with the ability to develop marginal teeth or cilia (both in the *Lophoziaceae* and *Ptilidiaceae*). It is possible therefore that the occurrence of such features represents a retention of a common ancestral feature, rather than independent new "acquisition."

The pachydermous cells of the leaves, as well as the cell-size and the oil-

---

91 The genus needs critical study, especially as regards its separation from the antipodal *Chandonanthus* Mitt. Andrews (1948) reports that study of the group in the Stephani herbarium demonstrated that the species under this generic name represent an unnatural aggregation of forms.

92 The insertion is not quite transverse, but varies from about 5-15° succubous, and the actual line of insertion is somewhat convex (towards the stem apex), much as in *Orthocaulis.* If the figures here given for *Temnona* (4:7,10) are compared with those given for *O. quadrilobus* by Buch (1933) a striking similarity is obvious, indicating a very definite and close relationship. The relationship becomes more obvious when impoverished modifications of *T. setiforme* are studied (such as the "variety" *alpinum* (Hook.) Frye and Clark). Such impoverished small forms represent a mod. *parvifolia-integriloba,* and have the leaves less deeply lobed, often only 3-lobed (then with the ventral lobe divided, and the dorsal much larger, as in the more typical species of *Orthocaulis:* compare 4:7 and 2:5-6). Such small forms of *setiforme* also generally have the leaves less deeply, and often merely 2/3 divided. Such small forms, which lack all or most of the marginal cilia or teeth of the lobes, are strikingly similar to well-developed forms of *Lophozia* (*O.*) *quadrilobus,* which have the leaves divided to a maximum of 2/3.

bodies are of the *Orthocaulis*-type, and offer no separation, but in the very deeply pluriplicate perianth the genus departs widely from *Orthocaulis* and other Lophozioid genera. This feature is to be interpreted as a secondary feature.

The genus thus departs from the *Orthocaulis*-like ancestral type chiefly in that: the lateral leaves become fixedly 4-lobed to within one-sixth of the base; the perianth becomes sharply multiplicate (7-10 times) to the base; in the channelled lobes and recurved margins of the leaves, the latter developing accessory teeth; and in the lack of gemmae.[93]

Species.—Temnoma setiforme (Ehrh.) Howe (Pl. 4).

GYMNOCOLEA Dumort.

(Plate 26)

Although not recognized for many years after its description by Dumortier in 1835, the genus was revived by Müller in 1910, and has been almost universally accepted since. It therefore offers no particular problem, except as regards its relationships. Müller (1910, p. 740) suggests it is related to *Leiocolea* "which includes species with at least entirely similar leaves." Buch (1933) does not treat the genus, and its closer relationships have been completely neglected, most writers laying emphasis on its isolation, because of the perianth-form.

The relationship believed to occur to *Leiocolea* does not exist, in my estimation, for the following reasons: the stem is merely 6-8 cells high in *Gymnocolea;* the leaf-cells are non-collenchymatous, with the walls becoming equally thickened; the oil-bodies are small and numerous; the ventral stem-sectors are generally only 1-3 cells wide (26:5) and normally develop at most rudimentary underleaves on sterile shoots (26:4); the capsule-wall is merely 2-stratose and has the thickenings of the inner wall quite different; rhizoids extremely few and scattered; leaves inserted more obliquely, less horizontally (26:8).

The above characters that isolate the genus from *Leiocolea,* however, almost all indicate a direct relationship to *Isopaches* Buch emend. K. M. In both groups the stems are reduced, and generally 7-8 cells high, and show no dorsiventral differentiation; both groups have non-collenchymatous and nearly or quite smooth leaf-cells that are able to develop only slight trigones but thick, obvious, often brownish walls; the oil-bodies are of about the same size and moderately numerous in both groups; the ventral stem-sectors are equally reduced and normally equally unable to produce discrete underleaves; in both groups the capsule-wall has become reduced to the bistratose condition (and

93 I have studied the stem-anatomy of *Temnoma setiforme;* it is nearly identical to that of *L.* (*O.*) *kunzeanus,* hence not figured. The cortical cells are relatively thick-walled and brownish, grading gradually into the less thick-walled medullary cells, which are somewhat larger; the stem is 14-15 cells high or more (as in 1:5) and shows, as is to be expected, no distinct dorsiventral differentiation of the medulla. As in *Orthocaulis,* the ventral 2 (or 3) layers of medullary cells are slightly smaller than the dorsal medullary cells. This I have already indicated as being the normal condition in the genera with a supposedly uniform medulla.

in no other related Lophozioid group!), with the tangential bands incomplete to vestigial (*Isopaches*) or nearly absent (*Gymnocolea*).

Gymnocolea differs from *Isopaches* chiefly in the non-plicate, anomalous, caducous perianths, in the obtuse to rounded-lobed leaves (usually acute-lobed in *G. acutiloba*, however), in the very sparse rhizoids, in the small non-dentate perichaetial bracts that scarcely invest the perianth at base, and in the presence of a single antheridium in the axils of the perigonal bracts. These differences, although indicating a more or less isolated position for *Gymnocolea*, do not make the very positive resemblances to *Isopaches* less important. Unlike *Isopaches* and other known *Lophozioid* genera, the tangential bands of the inner capsule-wall have been nearly or quite lost, resulting in only radial bands ("nodular thickenings"). *Gymnocolea*, like *Isopaches*, gives the impression of a reduced form. Unlike *Isopaches*, it has developed so many peculiarities that it can scarcely be retained as a subgenus of *Lophozia*.

Gymnocolea is generally described as lacking gemmae in the literature as recently as Frye and Clark (1945, p. 367). However the gemmae of this genus, which do not differ fundamentally from those of *Isopaches* in size and form, have been described.

North American species.—*Gymnocolea inflata* (Huds.) Dum. (Pl. 26).

ANASTREPTA (Lindb.) Schiffn.

Anastrepta was first segregated from the portmanteau genus *Jungermania* (*Lophozia*) as a subgenus by Lindberg in 1889; Schiffner, in 1893 then raised it to questionable generic rank. It has since been uniformly accepted as a discrete genus, hence offers no special taxonomic problems. The genus can be regarded as probably a specialized derivative form near *Lophozia*. It differs from *Lophozia*, and all related Lophozioid genera as follows:

Stems nearly erect to ascending in growth; ventral stem-sectors reduced, merely 2-3 cell-rows broad, generally unable to develop underleaves (except near inflorescences). Rhizoid mat dense. Leaves with insertion anomalous: the dorsal half extremely oblique and decurrent on the dorsal surface of the stem, the ventral portion becoming nearly (but not quite) transverse; leaves with entire postical[94] margin broadly and strongly reflexed, and the dorsal margin slightly so: therefore (and partly because of the nature of the insertion), strongly adaxially convex, appearing rather stiffly inserted and strongly distichously spreading on each side; leaves uniformly bilobed by a shallow, obsolete, rounded sinus for 1/12-1/10 their length. Cells distinctly collenchymatous, with well-developed trigones; oil-bodies 3-6 or even 8-16 per cell, spherical to ovoid, pellucid, 2-4 μ, either simple and homogeneous, or formed of several distinct smaller oil-globules (approaching the "grape-cluster" type).[95] Gemmae abundant, polygonal.

94 Frye and Clark (1945, p. 337) mistakenly say "dorsal margin."

95 K. Müller, (1910, p. 754) first described them as "1-2 per cell"; his Fig. 12, plate XIV (1939) clearly show 3-10 oil-bodies per cell, that are either homogeneous or show 1-4 included smaller oil-spherules.

Sporophyte with wall 5-stratose, the inner layer with annular bands.[96] Antheridia 1-2 per bract, with intermingled polymorphous paraphyses.

The differences from *Lophozia* (s. lat.) are largely in the peculiar leaf-insertion, and in the strongly reflexed ventral leaf-margins (resulting in an adaxially convex leaf). In *Lophozia* the leaves are generally adaxially more or less concave (15:6), but become distinctly convex in *L. rutheana* (5:1). Unlike all other genera of Lophoziaceae except the anomalous *Mesoptychia, Anastrepta* has the leaf-lobes vestigial. The genus, in this respect appears to approach the Jungermaniaceae, (especially *Nardia* and *Jamesoniella,* in which shallowly emarginate or retuse leaves are frequent). It differs from these genera in the rest of its organization (5-stratose capsule-wall; leaf-form; gemmae; dentate bracts, etc.), and is to be interpreted as an independent and parallel developmental line towards entire leaves.

North American species.—Anastrepta orcadensis (Hook.) Schiffn.[97]

MESOPTYCHIA (Lindb. & Arn.) Evs.[98]

(Plates 27-28)

The genus *Mesoptychia* represents an extremely isolated element in the Lophoziaceae. The presence of a well-developed perigynium occurring at right angles to the stem is the most important generic character of the genus (though it is not even mentioned in the generic diagnosis of Frye and Clark, 1943, p. 305); such a perigynium does not recur again in the family, except in the perhaps even more sharply isolated genus *Acrobolbus. Mesoptychia* differs from *Acrobolbus* (and almost all other North American genera of Jungermaniales, except the unrelated *Arnellia*) in retaining a well-developed perianth at the summit of the pendent, rhizoidous perigynium (28:6). The genus differs further from *Acrobolbus* in that there are very well-developed underleaves produced by the broad ventral merophytes of the stem (27:7-8; 28:4); in the more robust stems that are over 12 cell layers high (27:4,11); in the extremely shallowly bilobed leaves (27:1-2,5-6; 28:2,5); and in the fact that the calyptra is free from the perigynium-wall (28:6). Study of the sporophyte and of the living cell will undoubtedly disclose other important differentiating characters, but these structures were not available for comparative study to the writer. *Mesoptychia sahlbergii,* the only known species, differs from *Acrobolbus rhizophyllus Sharp* (the only North American species of

96 Frye and Clark (1945, p. 397) imply that all five layers have annular bands; these do not occur in the outer layer, however.

97 An oceanic species in most of its range, occurring in North America apparently as a rarity in Alaska, but nowhere else.

98 This combination dates from 1903, when Evans proposed elevating *Mesoptychia* to generic rank, in the Ottawa Naturalist (17:1-5); Müller 1910, pp. 618, 587, 716 also accepted the group as a genus. For some unknown reason, however, Frye & Clark date the genus from 1938, when it was listed in Annales Bryologici 10 (1937):4. Lindberg and Arnell had originally proposed the group as a subgenus of the collective genus *Jungermannia* (= *Lophozia* of the non-Scandinavian botanists) in 1889.

Acrobolbus) also in the inability to develop rhizoids from the marginal leaf-cells, as well as in the much greater robustness.

Frye & Clark place the genus in their "tribe" Nardioideae, together with such totally unrelated elements as *Mylia* and *Pedinophyllum*. The genus, however, has many distinct Lophozioid features—as recognized by Lindberg and Arnell (1889), Evans (1903) and by Müller (1940); the latter author formally put the genus in the family Lophoziaceae. The more obvious Lophozioid features are the uniformly, though shallowly bilobed leaves (27:1-2,5-6), as well as the broad ventral stem-sectors that develop large, bifid, pluriciliate underleaves on sterile as well as fertile shoots (27:7-8; 28:1,4); finally the irregularly scattered rhizoid-initials, the large size of the perigonal bracts (which are subequal in size to the normal vegetative leaves, 27:1-2; 28:3), and the intercalary eventual position of the androecium (e.g., lack of specialized form and occurrence of the androecia) are all features which indicate the genus is related to the Lophoziaceae. The leaf-cells are also obviously collenchymatous, generally forming strongly bulging trigones: a feature typical of (though not peculiar to) the Lophoziaceae. Finally, the facies of sterile plants is obviously "Lophozioid," and quite unlike that of the Jungermaniaceae or Plagiochilaceae (e.g. the "Nardioideae" of Frye and Clark). The Jungermanioid or "Nardioid" genera all agree in having minute or no underleaves (never bilobed and ciliate) and narrow ventral stem sectors, and in having entire, occasionally retuse leaves. Frye and Clark (1943, p. 267) state that their Nardioid group includes genera with "essentially unlobed alternate leaves." *Mesoptychia* would scarcely agree with this diagnosis. Frye and Clark further appear to have quite misunderstood the genus, since they separate it (in their key, p. 268) from *Pedinophyllum*, on the basis of the supposedly "transverse to little succubous" leaves of *Mesoptychia* vs. the "quite succubous" leaves of *Pedinophyllum*. As is indicated by 27:1-2 and 28:2, the leaves in *Mesoptychia* are extremely obliquely inserted, except for the arched lower part of the line of insertion. The sterile shoot, both in leaf-form, and in the very oblique line of insertion, is strongly reminiscent of the subgenera *Leiocolea* and *Barbilophozia* (of *Lophozia*); compare for instance 8:1-4 (*L. barbata*) with 5:1,4-7 (*L. schultzii*) with 27:1-2,5-8 (*M. salhbergii*). The resemblance in leaf-form between *L.* (*Leiocolea*) *schultzii* and *Mesoptychia* is particularly striking.[99]

It seems probable, therefore, that *Mesoptychia* can be derived from an unspecialized *Orthocaulis*-like type with large underleaves, that had developed the following *Leiocolea*-like features: very oblique, subhorizontally inserted, uniformly and shallowly bilobed leaves. The essential derivation from an unspecialized type of this kind would lie in the evolution of the perigynium, at right angles to the axis of the stem. This formation of a perigynium has, as is well known, developed repeatedly in such families as Southbyaceae. Marsupellaceae and Jungermaniaceae, etc.—entirely homoplastically. It is very

99 The immature perianth of *Mesoptychia* is described as beaked; if this is correct the similarity to *Leiocolea* may prove more than coincidental.

probable that the development of the perigynium in *Acrobolbus* and *Mesoptychia*, the two Lophozioid genera undergoing this type of modification, has proceeded quite independently, e.g., the common ancestral type had no perigynium.

The genus may be briefly diagnosed as follows:

Plants robust, large, 3.5-4.5 mm wide or more, decumbent to suberect in growth, sometimes caespitose. Stem normally 15-16 cells high or more in cross-section, showing a ventral medullary region composed of somewhat smaller cells, in 6-9 cell-layers, merely 18-24 (27) μ in diameter; dorsal medullary cells circa 24-32 (38) μ; ventral portion of medulla not mycorrhizal, gradually grading into the dorsal region (27:4,11); cortical cells little thick-walled, elongate, 3-5 x as long as wide, 18-20 μ wide on an average dorsally. Rhizoids rather numerous, scattered. Ventral merophytes broad, occupying 1/5-1/4 of the perimeter of the stem, developing large, bifid, pluriciliate underleaves (27:7-8; 28:1,2,4). Lateral leaves uniformly, shallowly bilobed, much broader than long (27:1-2,5-6; 28:2,5), the width from 1.2-1.3 or more the length of the ventral lobe; sinus obtusely angulate to rounded, descending for about 1/10-1/8 the leaf-length, dividing the leaf into a large ventral and much smaller dorsal lobe; ventral lobe broad, the ventral half of the leaf as a whole ovate, the apex rounded to obtuse (27:9); ventral half of leaf flat to slightly concave adaxially; dorsal "lobe" represented by a mere small, acute tooth on what appears to be otherwise an entire, obliquely ovate-triangular leaf, terminated generally by 1-2 or more cells forming an apiculum: dorsal half of leaf strongly adaxially convex, forming an oblique convex dorsal fold, the antical leaf-margin thus moderately to strongly reflexed.[100] Leaf-insertion extremely oblique, the lower portion somewhat arched, the upper half or more nearly horizontal, more or less obliquely decurrent on the lateral merophytes. Leaf-cells thin-walled, distinctly to strongly collenchymatous, the marginal cells averaging 25 μ in the lobes; median cells of lobes 23-32 μ (average 28 μ); cuticle rather weakly verruculose; oil-bodies undescribed (27:9,10). Gemmae unknown.

Dioecious. Perichaetial bracts like leaves, except for somewhat larger size and more obvious apiculate lobes; bracteole similar to the underleaves but larger and less deeply lobed and less ciliate.[101] Perianth well-developed, occurring at the crest of a well-developed rhizoidous perigynium, at right angles to the axis of the gametophyte, its height (before maturity) equal to

---

100 The convex dorsal fold of the antical portion of the leaf may have given the genus its name, which literally means middle-fold. Frye & Clark (1943, p. 305) think the dorsal fold of the perianth is referred to by the generic name.

101 Frye & Clark (l.c., p. 305) describe the bracteole as "similar to the leaves but larger" and again as "similar to the bracts, larger"—apparently in error. The bracteole is usually larger than the underleaves below it on the shoot, but never becomes larger than the lateral leaves or the associated bracts. The inferior size of the bracteole appears to be a constant feature of all anisophyllous Jungermaniales.

that of the fleshy perigynium (28:6);[102] perianth-mouth shortly beaked and suddenly constricted, the beak formed of short cilia 3-4 cells long.

Antheridial plants like sterile plants, except for the androecial regions (27:1-2). Androecia formed of 4 or more pairs of bracts, at first terminal (27:1), but by subsequent terminal growth becoming intercalary. Bracts similar to leaves, but the antical half of the leaf-base strongly ventricose, and antical base produced into a distinct, often dentate or ciliate small lobe (27:1; 28:3); antheridia therefore limited to the axils of the dorsal half of the bracts, which are modified, while the rest of the bracts are quite similar to leaves. Antheridia generally 2, rarely 3 per bract, ivory write;[103] antheridial stalk biseriate.

Nearctic Species.—Mesoptychia sahlbergii (Lindb. & Arn.) Evs.; the genus is monotypic. (An extreme Arctic-alpine species, known from Siberia (Jenissai River, type), eastward to Alaska, the Yukon, and Ellesmere Island. I have seen no Nearctic material, but have examined, through the courtesy of Dr. H. Persson, material from the Lena River, Siberia).

ACROBOLBUS G. L. & N.

Acrobolbus was first proposed in 1844 because of the very obvious densely rhizoidous perigynium that occurs at right angles to the stem. The perigynium is much better developed than in the very doubtfully related genus *Mesoptychia*, and no trace of a perianth is retained.

The genus is very poorly known, since the anatomy of the capsule-wall, the spore-elater ratio, and the nature of the oil-bodies is uninvestigated. Not knowing these, the position of the genus in the Lophoziaceae is open to question. One of the characteristics indicating a position of the genus among the Lophoziaceae is the ability to develop occasional 3-lobed leaves (noted by Sharp, 1936, for the Nearctic *A. rhizophyllus*).

Nearctic species.—A. rhizophyllus Sharp. The species is an endemic at high elevations in the Smoky Mts. in Tennessee and North Carolina. The

---

102 As far as I am aware, only the immature perianth is known. The figure 6, in Plate 28 is based on Evans (1902), and is the only illustration in the literature of the female plant. Fertile female plants were not present in material studied by the writer.

The immature perianth is described as more or less laterally compressed, slightly so ventrally and there with an obtuse, rounded fold, more distinctly so dorsally, and there with a sharper fold or blunt carina.

The writer wonders whether the lateral compression of the perianth may not be due to drying of the plants under pressure. If the species has a laterally compressed perianth normally, with dorsal and ventral keels, the genus should perhaps be removed from the Lophoziaceae to the Plagiochilaceae. Since the bulk of the other characters clearly ally the genus to the Lophoziaceae rather than Plagiochilaceae, the writer tentatively retains the genus in its present position.

103 Frye & Clark (l.c., p. 305) state "Antheridia up to 16." I have never seen more than 3 antheridia per bract, and to my knowledge none of the Jungermaniales ever have as high as 16 antheridia per bract.

rather fragmentary material has been well described and illustrated by Sharp (1936), except for the critical oil-bodies, which are not mentioned. The stem is merely 6-7 cells high in the species and shows no dorsiventral differentiation of the medulla, nor is the cortex distinctly differentiated from the medulla. The most obvious feature of the species (separating it from all other Nearctic Hepaticae) is the ability to develop numerous marginal rhizoids from the edges of the leaves. The generic position is still questionable, since the species is known only on the basis of sterile material.

Summary

An attempt is made to reclassify the supraspecific groups of the family Lophoziaceae. The subjective nature of the terms "genus" and "subgenus," together with the great disparity in rank between the various categories within the family makes a consistent classification very difficult.

The basic phylogenetic relationships of most of the groups (except for such monotypic genera as *Mesoptychia* and *Acrobolbus*) can in general be indicated with a fair degree of probability. The conclusions regarding relationships arrived at by the writer are graphically expressed in Tables I-II.

In Table I the genera and subgenera (and species in a few cases) are arranged in a sequence to show the polyphyletic reduction of the ventral stem-sectors. It is presumed that evolution was from an ancestral form not too dissimilar to *Herberta* (i.e., with oil-bodies, with a pluristratose capsule-wall, with very large, bilobed underleaves, with collenchymatous cells, and with terminal perianths, and with the archaic bilobed leaf-type of the early Jungermaniinae).

From such an unreduced, robust ancestral type evolution proceeded in the general direction of reduction in both gametophyte and sporophyte. In this table is stressed the parallelism that makes a classification of the complex difficult. From a relatively unreduced Lophozioid type (which we may call the *Orthocaulis kunzeanus* type), the family has undergone modification in several basic ways:

1. The ventral stem-sectors have become reduced (associated in general with a more horizontal mode of growth).

2. Correlated with 1, there has of necessity been reduction (and in the more extreme cases) loss of the underleaves.

3. With reduction in size the axis of the gametophyte gradually becomes composed of fewer rows of cells.

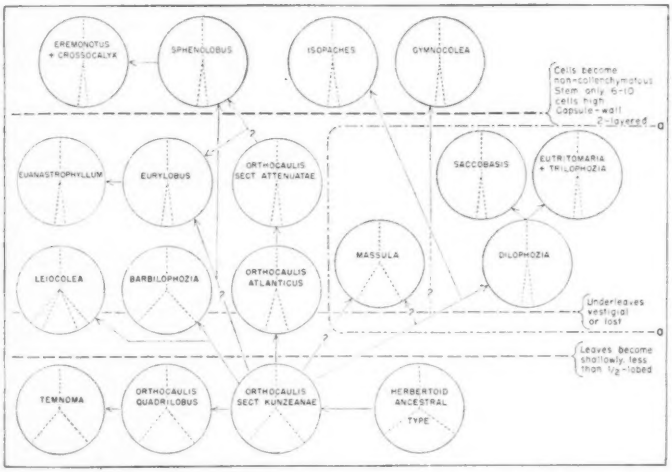
4. With reduction in size of the gametophyte the sporophyte of necessity undergoes reduction in size. In several cases (*Crossocalyx, Sphenolobus, Gymnocolea, Isopaches*) the sporogonium wall is reduced to the bistratose condition. In extreme cases (*Crossocalyx, Eremonotus*), the axis of the sporophyte, or seta, is reduced to 4 inner and 8 outer rows of cells.

In Table I the degree of preservation of the ventral stem-sectors is schematically indicated. A hypothetical stem-cross-section is given for each group, and the degree of development of each of the three stem sectors is indicated.

In Table II an attempt is made to illustrate the probable phyletic relationships of the chief groups. An effort is made here to indicate the parallel and unrelated groups by means of horizontal and vertical lines that serve to draw together the morphologically more similar groups.

Diagram I is based on the same assumption used by Buch (1933, p. 296), namely, the oldest acrogynous Hepaticae had three equal rows of bilobed

TABLE I



leaves. As Buch points out, the predominance of a 3-sided apical cell and corresponding development of 3 rows of stem-segments, together with the constantly bilobed form of the embryonic leaves, makes such a supposition warranted. In looking for an archetype, a type like *Herberta* seems to approach nearest the Lophozioid archetype, but differs in: the perianth form, the specialization of the leaves and other characters. The Herbertaceae cannot therefore be looked upon as the ancestral forms for the Lophoziaceae, even though they indicate what form the archetype probably took. In further characterizing such an archetype we are probably justified in concluding that:

1. The leaf-cells were collenchymatous (this appears to be the primitive condition throughout the acrogynous liverworts).

2. The sporophyte was relatively unreduced, and had the "type general" of the seta (Douin, 1908), and a multistratose capsule wall. The fact that a 5-7-stratose capsule-wall and simple (unreduced) form of the seta exist in the Herbertaceae is significant.

3. The antheridial stalk consisted of 2 rows of cells.

4. The leaf-lobes were not strictly fixed, but the number determined in part by environmental conditions. (In this the writer differs from Buch.) I think the ability to develop supplementary leaf-lobes is a "primitive" characteristic. It recurs again so often in various "low" families, such as Ptilidiaceae, Lepidoziaceae, Herbertaceae (*Lepicolea*, if that genus belongs here), Trichocoleaceae, as well as in the Lophoziaceae, that it must be regarded as primitive. In the Lophoziaceae the retention of wide ventral stem-sectors, a primitive character, is correlated under all conditions with the ability to develop accessory leaf-lobes, as in *Orthocaulis, Temnoma, Barbilophozia,* and *Massula*—(only in Leiocolea is there an exception to the rule). If this assumption is accepted (and it must be, if *Orthocaulis* is taken as the most synthetic, hence archaic type), then the derivation of the various 2-lobed types as well as the 3-4-lobed types is relatively simple.

5. The original leaf-insertion was a nearly straight line that, though not transverse, was only a little succubously oblique (such a leaf-insertion, for the lateral leaves, appears to have been achieved in almost all of the lower acrogynous liverworts, except for the incubous-leaved forms). The nearly horizontal or extremely oblique leaf-insertions found in *Barbilophozia, Leiocolea* and *Massula* are derived readily from such a type, while the *Anastrophyllum* and *Tritomaria* types are also readily derived from it. Such a type exists in some *Orthocaulis* species.

6. The oil-bodies were moderate in size (4-9 μ) and moderately numerous per cell (6-15 or so). Deviations from this type are always accompanied by other specialized features (note *Massula* and *Leiocolea*).

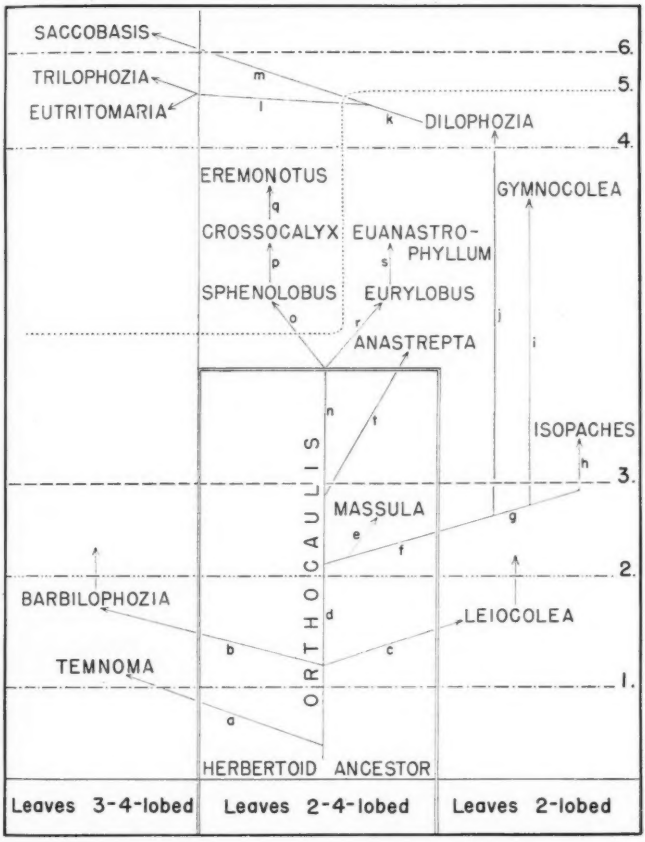
With these assumptions the relationships expressed in Table II become intelligible. It is presumed in Table II that a certain amount of parallel development has occurred, concurrently with parallel increase in dorsiventrality, resulting in the existence of diverse groups on identical "developmental" levels. From this parallelism has come the difficulty in classification of the complex. The parallel steps may be listed as follows (corresponding with the numbers on Table II.):

1. The original isophylly gives way to a distinct anisophylly, but very large underleaves are retained; no retention of antheridia in axils of underleaves; leaves acquire a barely perceptibly succubous line of insertion; the stem retains a suberect type of growth and lacks differentiation of the medulla.

2. The ventral stem-sectors remain wide (6 or more cells in width), but lose the ability to develop underleaves on sterile shoots; anisophylly becomes therefore extreme and the plant becomes completely bilateral; the ability of the leaves to develop basal cilia is also lost.

3. The ventral stem-sectors become reduced in width (usually merely 1-2 cells wide; locally, especially where endogenous buds are laid on, more cells wide), and there are never discrete underleaves.

TABLE II



4. The stem, with increasing dorsiventrality, becomes dorsiventrally differentiated, with the medulla developing a small-celled ventral band of mycorrhizal-nutritive cells.

5. The upper portion of the leaf-insertion loses any tendency to be inserted in a line curving towards the stem-base (i.e., it becomes transverse or even curves towards the stem apex).

6. The dorsal half of the leaf-insertion becomes curved towards the stem-apex.

The various specializations that cut off the individual groups or lines may be briefly summarized, corresponding to the letters in Diagram II.

a. The leaves become extremely deeply lobed and uniformly 4-lobed; the perianth becomes deeply pluriplicate to base.

b. The leaves become nearly horizontally inserted; cilia of the leaf bases become formed by elongate cells; the leaves become 4-lobed.

c. The leaves become nearly horizontally inserted; cilia of the leaf-base are lost (exc. in *L. schultzii*); the leaves become fixedly 2-lobed; leaf-cells tend to become very large; oil-bodies become large and few; perianth becomes beaked.

d. Leaves become usually fixedly 2-lobed; underleaves are lost (exc. *M. obtusa*); leaves become more oblique in insertion (generally?).

e. Cells become non-collenchymatous both in leaves and stems; stem-cells become narrow and elongate (usually?); oil-bodies become minute and numerous; leaves retain ability to form 4-5-lobes; ventral stem-sectors stay broad (8 cells or more).

f. Ventral stem-sectors reduced to width of 1-2-cells; stem-cells do not become very narrow and elongate; oil-bodies remain moderate in size and number; leaves lose ability to develop other than occasional third lobe.

g. Cells become non-collenchymatous, equally thick-walled; stem becomes only 8-12 cells high: the medulla remains uniform.

h. Perianth remains plicate, persistent; gemmae commonly formed; leaves retain acute lobes; ♂ and ♀ bracts remain dentate.

i. Perianth becomes inflated, caducous; gemmae rare; leaves become obtuse-lobed; ♂ and ♀ bracts become entire-lobed.

j. Stems develop a dorsiventrally differentiated medulla, but remain 15-20 cells high normally; cells remain strongly collenchymatous, develop bulging trigones.

k. Leaves become fixedly 3-lobed; cortical stem cells become elongate dorsally; dorsal half of insertion of leaves becomes directed more towards stem-apex (never towards base); basal leaf-cells become very elongate.

l. Leaves remain asymmetric; cortical cells remain 2-3.5 x as long as wide; dorsal end of leaf-insertion remains transverse or nearly.

m. Leaves become symmetrical; cortical cells become extremely elongate; dorsal end of leaf insertion becomes directed towards stem-apex.

n. Ventral stem-sectors reduced to width of 1-2 cells (already occurring in *O. attenuata*); leaves become fixedly 2-lobed; dorsal half of leaf becomes more transversely inserted.

o. Dorsal half of leaf remains completely transverse in insertion; cells become non-collenchymatous, equally thick-walled; capsule-wall becomes 2-stratose; dorsal portion of leaf not expanded, the basal portion extending only to stem-midline; gemmiparous shoots become erect, slender, with appressed leaves.[104]

p. Seta becomes reduced to 4 inner, 8 outer rows of cells; gemmiparous shoots become extremely specialized; perianth acquires a distinct deep antical fold; stems become merely 6-7 cells high.

q. Ability to produce gemmae lost; cells become extremely small.

r. Dorsal end of line of insertion curves down and runs down the upper edges of the lateral stem-sectors, hence is not entirely transverse; cells remain collenchymatous; capsule-walls remain 3-4 stratose; dorsal portion of leaf expanded, extending more or less across the stem; gemmiparous shoots do not become modified; leaves remain relatively broad (much wider than long); leaf-lobes retain strong tendency to be incurved (as in ancestral *Orthocaulis*).[105]

s. Leaves become distinctly widest near base, become as long or longer than wide; ability to produce 3-lobed leaves lost; cells become very strongly collenchymatous; leaves become strongly canaliculate.

In conclusion it should be stated that the continuum existing (in general) between the various groups is clearly indicated in the diagram. *Barbilophozia* runs into *Orthocaulis* (through *B. barbata*); *Orthocaulis* runs into *Temnoma* (through *O. quadrilobus*); *Massula* appears to run into *Barbilophozia* (through *M. obtusa* and *B. barbata*); *Orthocaulis* appears to run into *Anastrophyllum* (through *O. binsteadii* and *atlantica*, and *Sph. minutus* and *Eurylobus saxicolus*); *Dilophozia* appears to approach *Massula* (through *L. excisa*) and *Tritomaria* (through *L. longidens* and *T. scitula*). These intermediate or synthetic species make a clear-cut circumscription of genera very difficult (hence prompt conservative treatments, such as the one of Andrews, 1948). Very few of the groups are reasonably sharply cut off (among them *Massula, Leiocolea, Saccobasis, Gymnocolea*). The more conservative treatment in the preceding discussion therefore appears to be more desirable.

---

104 Whether this indicates any phyletic connection to such species as *L.* (*Orthocaulis*) *attenuatus, binsteadii,* and *atlantica,* in which there has already occurred reduction of the ventral stem-sectors and development of more or less slender erect gemmiparous shoots, is an open matter. The correlation is interesting at any rate, and indicates that there may be decided convergence here. It should be noted that the "lower" species of *Orthocaulis* do not have specialized gemmiparous shoots, and also retain underleaves and wide ventral stem-sectors.

105 The connection between *Orthocaulis* species (such as *binsteadii* and *atlantica*) and *A.* (*Eurylobus*) *saxicolus* seems significant. The leaf-insertion is strikingly similar; the ventral stem-sectors are equally reduced, and the leaves are broad and have incurved lobes. This similarity is emphasized by the fact that *A.* (*E.*) *saxicolus* still retains the ability to develop occasional 3-lobed leaves on sterile shoots, much as is the case in the two species of *Orthocaulis* mentioned. There thus seems obvious convergence towards the more specialized species of *Orthocaulis,* on the one hand, and the less specialized species of *Anastrophyllum,* on the other hand.

REFERENCES

ANDREWS, A. L. 1948—Taxonomic Notes, VII. The *Lophozia-Sphenolobus* Complex. The Bryologist 52: 33-37.

BUCH, H. (1931-1932) 1933—Vorarbeiten zu einer Lebermoosflora Fennoscandias. I. Ein Versuch zur Aufteilung der Gattungen *Lophozia* Dum. und *Sphenolobus* Steph. Memoranda Soc. F. et F. Fennica 8: 282-297, Figs. 1-2.

———1933a—Experimentell-systematische Untersuchungen über die *Lophozia ventricosa*-Gruppe. Ann. Bryol. 6: 7-14, Figs. 1-7.

———1933b—*Lophozia silvicola* Buch sp. nov. and *L. gracillima* Buch sp. nov., *in* Bryophyta Nova, Ann. Bryol. 6: 125-131, 23 Figs.

———1936—Suomen Maksasammalet. 116 pp., 35 pls., 1 map. Helsinki.

———1937—*Lophozia* (*Orthocaulis*) *atlantica* in Verdoorn, Hep. Selectae et Criticae. Ann. Bryol. 10: 126.

———(1941) 1942—Vorarbeiten zu einer Lebermoosflora Fennoscandias. VII. Über die verwandtschaftlichen Beziehungen zwischen den Arten der Gattungen *Sphenolobus* St. sens. lats. und *Lophozia* Dum. sens. lat. Memoranda Soc. F. et Fl. Fennica 17: 283-290, Fig. 6.

———, EVANS, A. W. AND FR. VERDOORN (1937) 1938—A Preliminary Check List of the Hepaticae of Europe and America (North of Mexico). Ann. Bryol. 10: 3-8.

CAIN, R. F. ET M. FULFORD 1948—Contribution to the Hepaticae of Ontario. Bryologist 51: 174-185.

CASARES-GIL, A. 1919—Flora Ibérica. Briofitas. Hepáticas. 775 pp., 399 figs.

DOUIN, CH. 1908—Le pedicelle de la capsule des Hepatiques. Bul. Soc. Bot. France 55: 194-202, 270-276, 360-376, pls. 6-9.

———1920—La famille des Cephaloziellacees. Mem. Soc. Bot. France 79: 1-90, pls. 1-9.

EVANS, A. W. 1893—Two new American hepaticae. Bull. Torr. Bot. Club 20: 307-310, pls. 162-163.

———1896—A note on *Jungermannia marchica* Nees. Bull. Torr. Bot. Club 23: 12-15, pls. 254-255.

———1900—Papers from the Harriman Alaska Expedition—5. Notes on the hepaticae collected in Alaska. Proc. Washington Acad. Sci. 2: 287-314, pls. 16-18.

———1902—Notes on New England hepaticae. Rhodora 4: 207-213.

———1903—Yukon Hepaticae. Ottawa Nat. 17: 13-24, pls. 1-2.

———1912—Notes on North American hepaticae—3. Bryologist 15: 54-63, pl. 2.

———1935—Recent segregates from the Genera *Lophozia* and *Sphenolobus*. The Bryologist 38: 61-70.

———1939—The Classification of Hepaticae. Bot. Rev. 5: 49-96.

FRYE, T. C. AND L. CLARK 1937-1947—The Hepaticae of North America. University of Washington Publ. Biol. 6(1-5): 1-1018.

HOWE, M. A. 1899—The hepaticae and anthocerotes of California. Mem. Torr. Bot. Club 7: 1-208, pls. 88-122.

JENSEN, C. 1915—Danmarks Mosser. Bryofyter—1. 317 pages, pls. 1-6. Kobenhavn.

JOERGENSEN, E. 1934—Norges Levermoser. Bergens Mus. Skrifter No. 16: 1-343, Maps 1-25.

LINDBERG, S. O. ET H. W. ARNELL 1889—Musci Asiae borealis—I. Lebermoose. Kongl. Svenska Vetens.-Akad. Handlingar 23(5): 1-69.

LOESKE, L. 1907—Bryologische Beobachtungen aus der Algauer Alpen von Loeske und Osterwald. Abhandl. Bot. Ver. Bradenburg 49: 30-65.

LORENZ, ANNIE 1910—Some Lophozias of the *ventricosa* group. Bryologist 13: 36-45, pls. 3-5.

———1910a—Notes on *Lophozia alpestris* (Schleich.) Evans. Bryologist 13: 69-71, pl. 8.

———1911—New England Lophozias of the *muelleri*-group. Bryologist 14: 25-31, pls. 4-5.

MACVICAR, S. M. 1926—The Student Handbook of British Hepatics, Ed. 2. Eastbourne, England xxix-464, illus.

MEYLAN, CH. 1924—Les Hepatiques de la Suisse. Beiträge zur Kryptogamenflora der Schweiz 6: 1-318, figs. 1-213.

———1939—Localité nouvelles pour la flore des Muscinées de la Suisse. Bull. Soc. Vaudoise Sc. Nat. 60: 261.

MÜLLER, K. 1905-1911—Die Lebermoose Deutschlands usw. Rabenhorst's Kryptogamenflora. 2 Ed. 6(1): i-vii, 1-870, Figs. 1-361, Leipzig.

———1939—Die Ölkörper der Lebermoose. Ber. Deutsch. Bot. Ges. 57: 325-370. Taf. XIV-XV.

———1939-1940—Die Lebermoose Europas. Rabenhorst's Krytpogamenflora 6 (Ergänzungs-band): 1-320, 26 Figs. Leipzig.

———1947—Morphologische Untersuchungen zur Aufklärung einiger europäischen Lebermoose. Beiträge zur Kryptogamenflora der Schweiz. 10(2): 1-55, figs. 1-3.

———1948—Der Systematische Wert von Sporophytenmerkmalen bei den Beblätterten Lebermoosen. Svenks. Bot. Tidsk. 42: 1-16, figs. 1-2.

NEES VON ESSENBECK, C. G. 1833-1838—Naturgeschichte der europäischen Lebermoose. 1: 1-348, 2: 1-500, 3: 1-594, 4: 1-540. Breslau.

SCHIFFNER, V. 1893—Jungermanniaceae akrogynae, *in* Engler-Prantl, Nat. Pflanzenfamilien 1(3): 61-134, figs. 36-70, Leipzig.

———1903-1905—Kritische Bemerkungen über die europäischen Lebermoose, usw. Sitzungsbericht des Deutschen naturw.medicin. Vereins für Böhmen "Lotos," 1903, Nr. 7: 3-6, 43-49, 61-63; 1905, Nr. 3: 24-34, 37-39, 45.

———1908—Ibid, V. Series. Ber. naturwiss.-med. Ver. Innsbruck, 23 (Beilage): 1-69, pl. 1.

SCHUSTER, R. M. 1949—Taxonomic and Ecological Notes on the Hepaticae of Central and Western New York. Amer. Midl. Nat. 42(3): 513-712.

———1950—Notes on Nearctic Hepaticae. II. The Hepaticae of the East Coast of Hudson Bay. The Canadian National Museum, Bull. 122.

SHARP, A. J. 1936—*Acrobolbus* in the United States. Bryologist 39: 1-2, pl. 1.

STEPHANI, F. 1902—Species Hepaticarum. *Sphenolobus* (Lindb.). Bull. Herb. Boissier II. 2: 164-179.

TURESSON, G. 1925—The plant species relation to habitat and climate. Hereditas.

VERDOORN, F. 1932—Manual of Bryology. The Hague.

WARNSTORF, C. 1903—Kryptogamenflora der Mark Brandenburg. I. Leber- und Torfmoose. Leipzig.

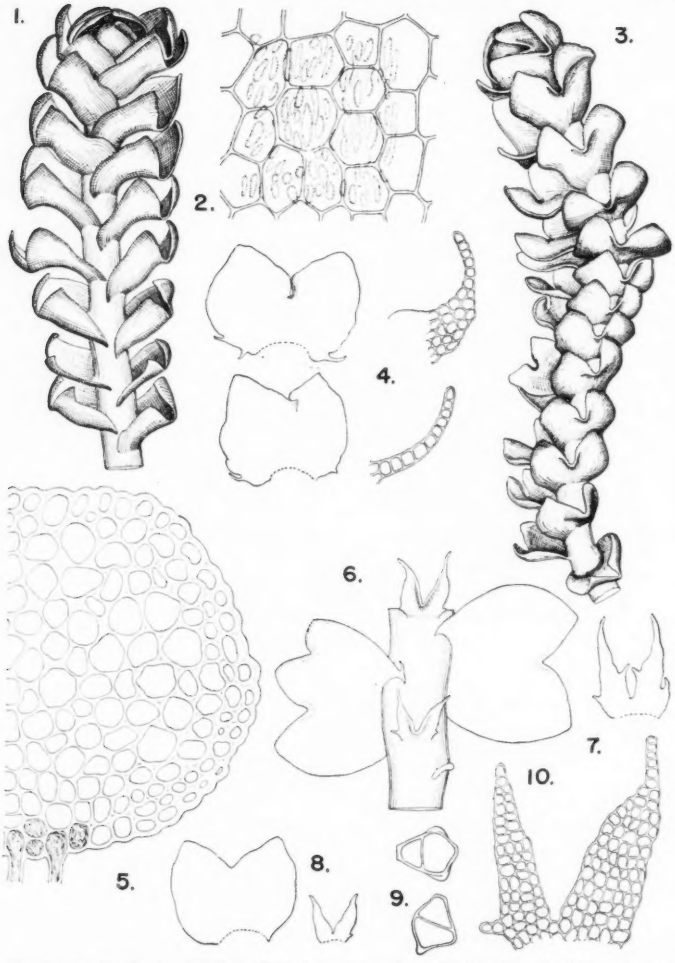


PLATE 1. *Lophozia* (*Orthocaulis*) *kunzeana*.—1. Dorsal view of shoot of mod. *plicata*. 2. Cells of leaf-middle, surface view, with cuticular papillae indicated in median area. 3. Lateral view of shoot. 4. Two leaves from below female inflorescence, to their right the basal cilia. 5. Cross-section of stem. 6. Postical view of part of robust shoot, somewhat flattened. 7. Underleaf of sterile shoot. 8. Normal leaf of sterile shoot, with associated underleaf to the right. 9. Gemmae. 10. Underleaf of sterile shoot. (Figs. 1, 3, 4, 5, 7, 8, 10 drawn from material collected by the writer on Big Susie Is., Susie Isls., Cook Co., Minn.; Fig. 2 from material collected by the writer at Grand Marais, Minn.; Fig. 6 from material from Belle Rose Is., Susie Isls., Cook Co., Minn., collected by the writer; Fig. 9 from Little Susie Is., Cook Co., Minn., collected by the writer). Fig. 1, 27.5×; 2, 332×; 3, 29×; 4, 21×; 5, 196×; 6, 23×; 7, 42×; 8, 23×; 9, 460×; 10, 94×.

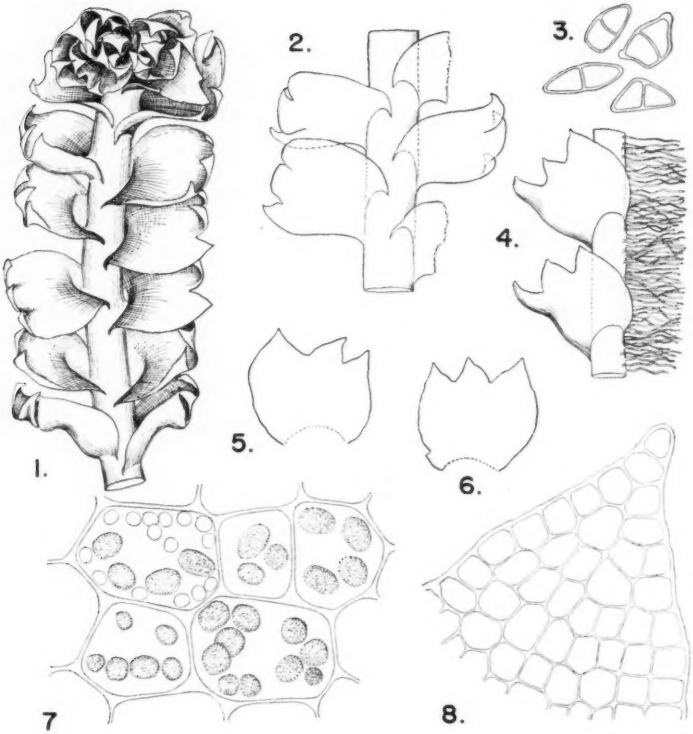


PLATE 2. *Lophozia* (*Orthocaulis*) *attenuata*.—1. Sterile, non-gemmiparous shoot. 2. Postical view of part of shoot, showing ventral stem-sectors 1-2 cells wide. 3. Gemmae. 4. Lateral view of part of shoot. 5-6. Two leaves. 7. Cells of middle of ventral lobe, with oil-bodies drawn in (and in upper left-hand cell, with chloroplasts). 8. Ventral lobe of leaf, showing cells. (Figs. 1-2, 4, Gunflint Lake, Cook Co., Minn., *Schuster;* Fig. 3, Blue Mt., N. Y., *Schuster;* Figs. 5-6, Raquette Lake, N. Y. *Schuster;* Figs. 7-8, Big Susie Is., Susie Isls., Cook Co., Minn., *Schuster*). Fig. 1, 23×; 2, 28×; 3, 300×; 4, 28×; 5-6, circa 30×; 7, 720×; 8, 350×.

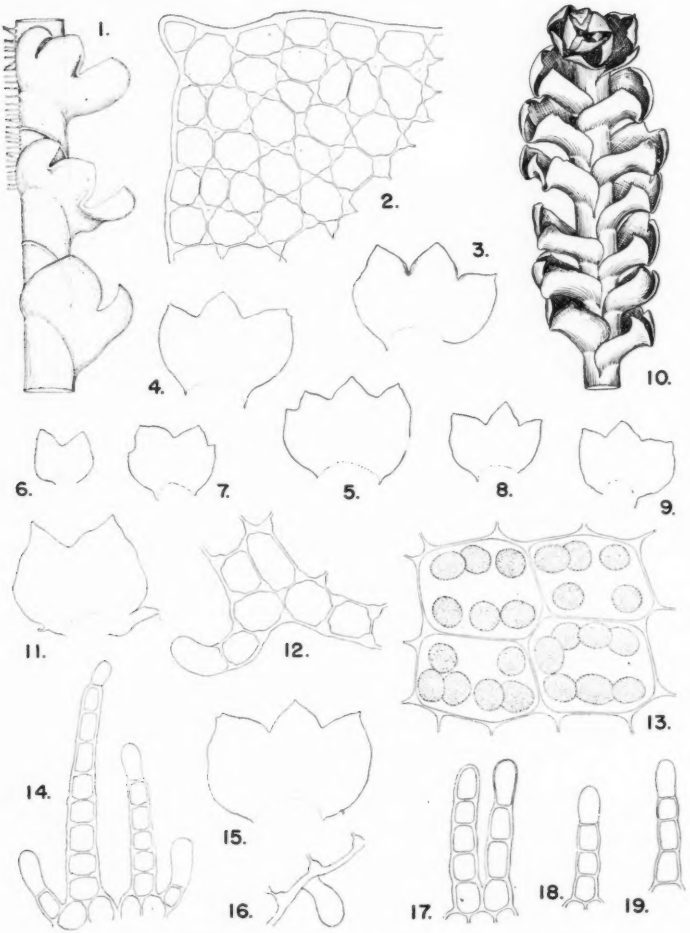


PLATE 3.—*Lophozia* (*Orthocaulis*) *atlantica*.—1. Lateral view of part of shoot, alternating leaves removed; rhizoids drawn in above only. 2. Ventral leaf-apex of leaf in Fig. 5. 3. 3-5. Leaves from a robust shoot. 6. Immature, juvenile bilobed leaf. 7-9. Leaves from a less robust plant. 10. Sterile shoot, dorsal view. 11. Large leaf. 12. Portion of dorsal base of Fig. 11, showing stalked slime papilla. 13. Cells of leaf-middle, showing oil-bodies. 14. Large underleaf. 15. Large, 3-lobed leaf, showing sessile slime-papilla of ventral margin. 16. Slime papilla of leaf in Fig. 15. 17-19. Underleaves of robust plant. (Figs. 1-10 drawn from plants collected on Mt. Washington, N. H. in July 1944, by *R. M. & O. M. Schuster;* Figs. 11-12, 14-16, from plants collected at the Great Whale River, Quebec, by *J. W. Marr, No. 665,* det. *R. M. Schuster;* Fig. 13 drawn from plants

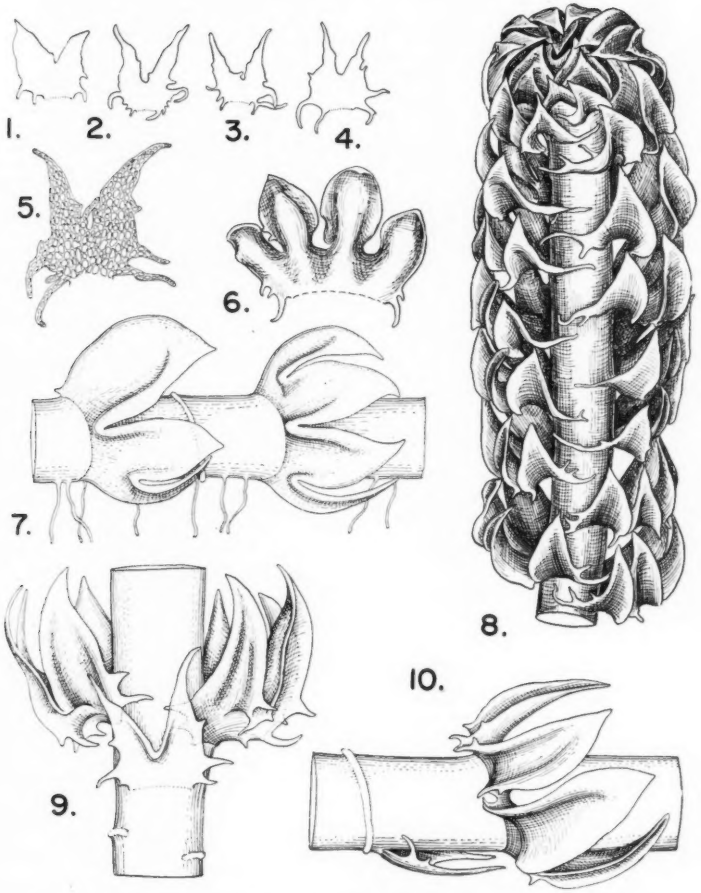


PLATE 4. *Temnoma setiforme.*—1-5. Underleaves. 6. Lateral leaf, adaxial view. 7. Lateral view of part of shoot, from a less robust plant, approaching the "var. *alpina.*" 8. Apex of normal shoot. 9. Postical view of section of shoot, rhizoids omitted. 10. Lateral view of part of shoot, rhizoids omitted. (All figures drawn from material collected by the writer on Mt. Washington, N. H.). Figs. 1-4, 40×; 5, 55×; 6, 30×; 7, 45×; 8, 30×; 9-10, 45.×.

---

collected at Great Whale River by *J. W. Marr, No. 655a,* det. *R. M. Schuster;* Figs. 17-19 drawn from plants collected on Big Susie Is., Susie Isls., Cook Co., Minn. by *R. M. Schuster,* from same plants figured on Plate 8, Figs. 9-14). Fig. 1, 24×; 2, 350×; 3-5, 24×; 6-9, 16×; 10, 20×; 11, 20×; 13, 650×; 14, 210×; 15, 20×; 17-19, 300×.

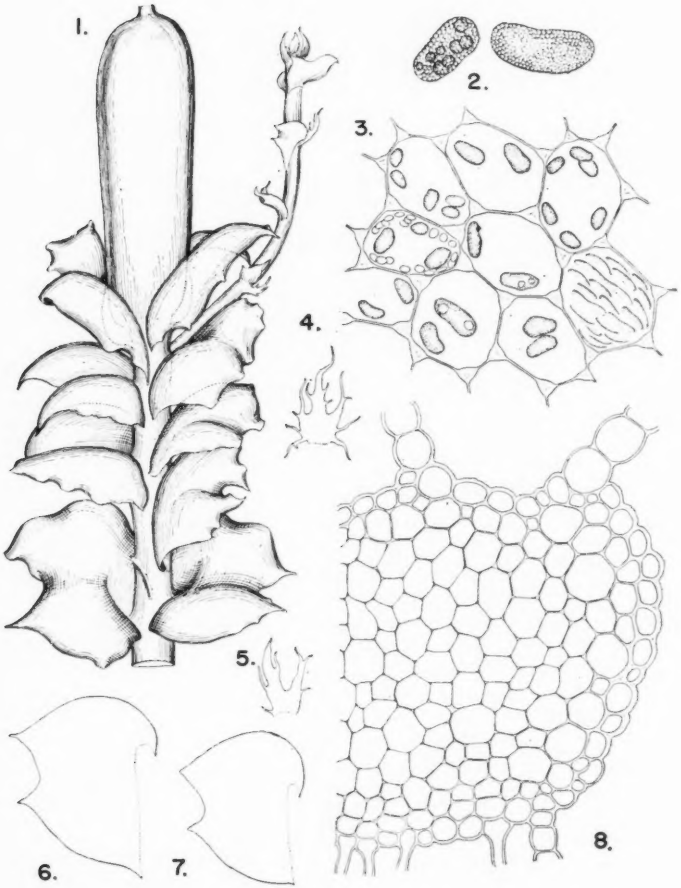


PLATE 5. *Lophozia* (*Leiocolea*) *schultzii* (*rutheana*).—1. Fertile shoot, showing ventricose perichaetial bracts in which antheridia occurred. 2. Two oil-bodies, the left one showing numerous inlcuded oil-globules. 3. Cells of leaf-middle (oil-bodies drawn in; one cell also showing chloroplasts; one cell showing cuticular papillae). 4-5. Two underleaves from sterile shoot. 6-7. Two leaves. 8. Cross section of stem. (All figures drawn from material collected by the writer at Grand Portage, Minn.). Fig. 1, 7.5×; 2, 940×; 3, 300×; 4-5, 8×; 6-7, 7.6×; 8, 75×.

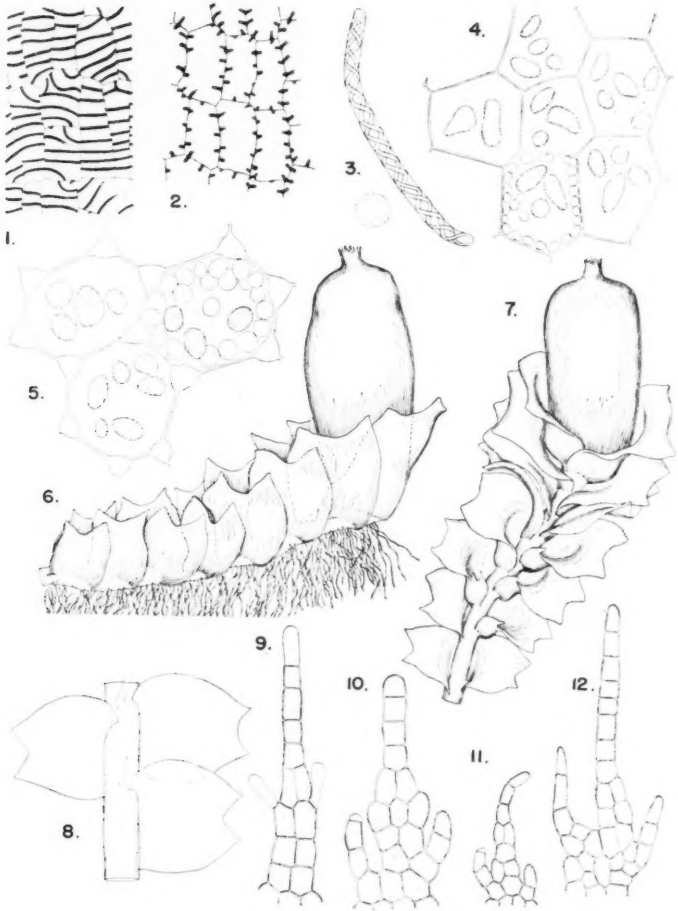


PLATE 6. *Lophozia* (*Leiocolea*) *badensis*.—1. Inner cells of capsule-wall. 2. Outer cells of capsule-wall. 3. Spore and elater. 4. Cells of leaf-middle, showing oil-bodies and (in one cell) chloroplasts. *Lophozia* (*Leiocolea*) *gillmani*. 5. Cells of leaf-middle, showing oil-bodies and chloroplasts (in right-hand cell). 6. Fertile plant, lateral view. 7. Same, dorsal view. 8. Sterile shoot sector, rhizoids omitted. 9-12. Underleaves, from sterile shoots. (Figs. 1-4 from material collected at Crystal Springs, Wisconsin, *Schuster*. Fig. 5 from Susie Isls., Cook Co., Minn., *Schuster*. Figs. 6-12, from Temperance River, Cook Co., Minn., *Schuster*). Figs. 1-2, 232×; 3, 360×; 4, 400×; 5, 660×; 6-7, 6×; 8, 8×; 9-10, 12, 130×; 11, 110×.

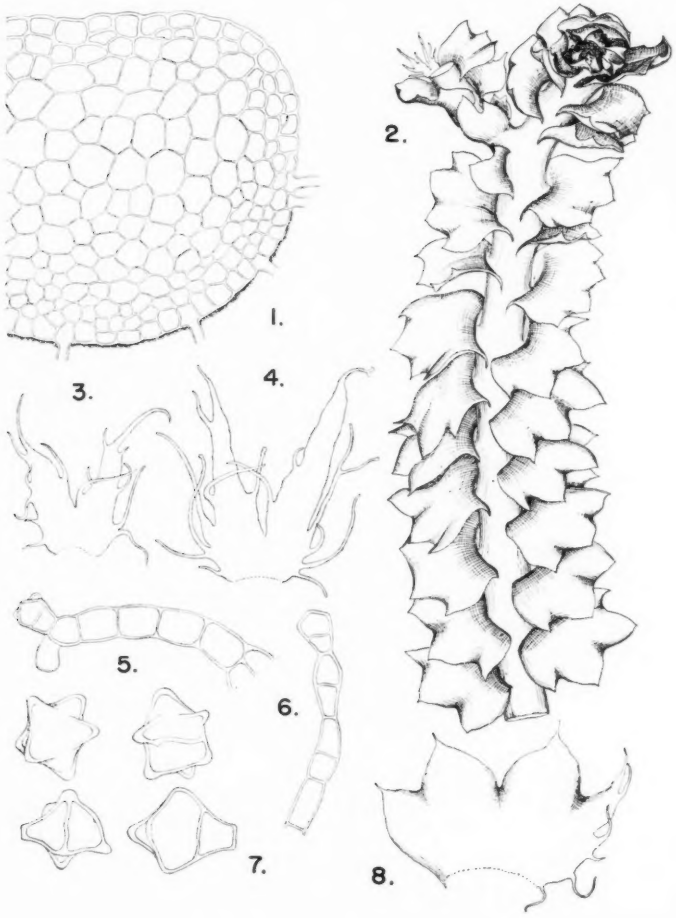


PLATE 7. *Lophozia* (*Barbilophozia*) *hatcheri*.—1. Cross-section of stem. 2. Gemmiparous shoot, showing lateral branch replacing ventral half of leaf. 3-4. Underleaves, the larger from gemmiparous apex of plant and showing gemmae-formation from tip of cilia. 5-6. Apices of cilia from underleaf in Fig. 4, showing gemmae-formation. 7. Gemmae. 8. Lateral leaf. (All figures from material collected by the writer at Gunflint Lake, Minn.). Fig. 1, 175×; 2, 18×; 3, 33×; 4, 42×; 5-6, 320×; 7, 575×; 8, 24×.

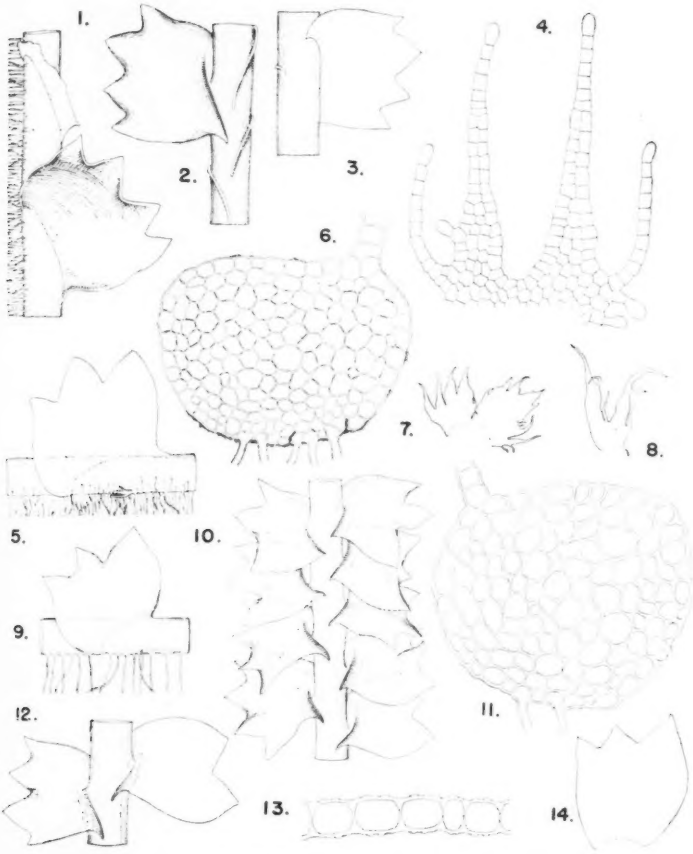


PLATE 8. *Lophozia* (*Barbilophozia*) *barbata*. 1. Part of shoot, lateral view, with bases of rhizoids drawn in. 2. Same, dorsal view. 3. Same, ventral view, rhizoids omitted. 4. Underleaf of sterile shoot. 5. Leaf, lateral view, showing attachment and rhizoids and underleaf. 6. Cross-section of stem. 7. Bract and bracteole (bracteole to left). 8. Underleaf of fertile shoot, from some distance below perianth. (Figs. 1-5, from Belle Rose Is., Susie Isls., Cook Co., Minn., *Schuster*. Fig. 6 from Gunflint Lake, Cook Co., Minn., *Schuster*. Figs. 7-8 from Peasleeville, N. Y., *Schuster*). Figs. 1-3, 12×; 4, 130×; 5, 17.5×; 6, 125×; 7, 5×; 8, 24×.

Lophozia (*Orthocaulis*) *atlantica* forma *eflagellis*. 9. Leaf, lateral view. 10. Part of robust shoot, showing 3-4-lobed leaves. 11. Stem-cross-section. 12. Part of shoot, dorsal view. 13. Cross-section of leaf. 14. Normal leaf. (Figs. 9-14. All from material from Big Susie Is., Susie Isls., Cook Co., Minn., *Schuster*). Fig. 9, 17.5×; 10, 19×; 11, 165×; 12, 17.5×; 13, 230×; 14, 23×.

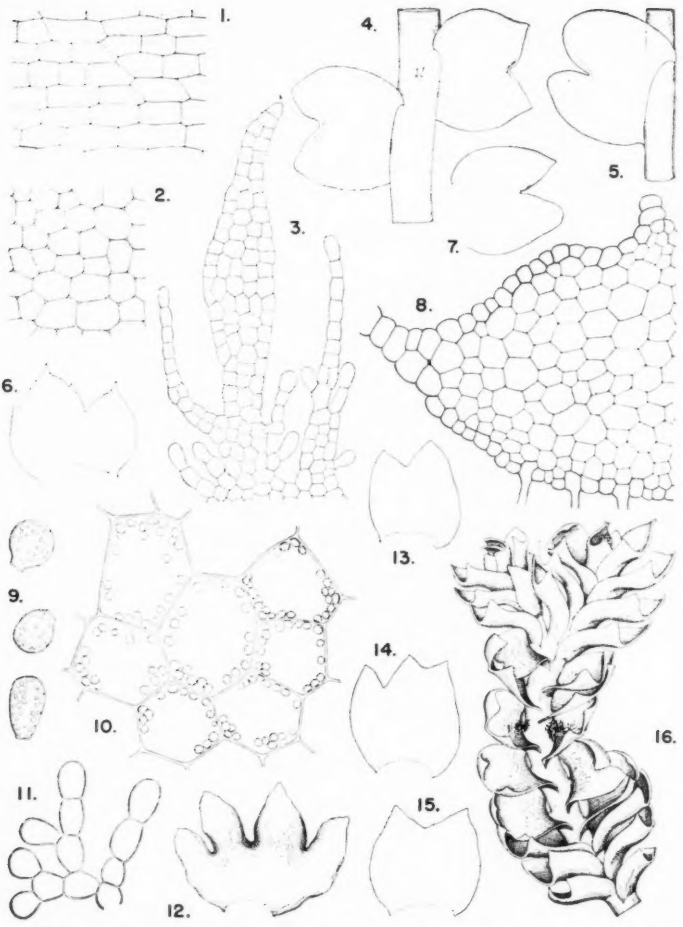


PLATE 9. *Lophozia* (*Massula*) *obtusa*.—1. Dorsal, cortical stem cells. 2. Basal leaf-cells (same magnification as Fig. 1). 3. Underleaf of sterile shoot. 4. Postical view of shoot-sector, showing underleaf, with rhizoids omitted. 5. Leaf, showing line of insertion. 6. Occasional dentate leaf. 7. Atypical, narrow leaf. 8. Cross-section of stem and leaf-base. *Lophozia* (*Massula*) *mildeana*. 9. Gemmae (from plant in Fig. 10). 10. Cells from leaf-middle, from a mod. *colorata-mesoderma*. 11. Gemmae-fascicle. 12. Leaf from a robust shoot. *Lophozia ventricosa* (approaching *confertifolia*). 13. Narrow leaf. 14. Trilobate leaf. 15. Normal leaf. 16. Plant, showing slight gemmae-development, of a mod. *colorata-pachyderma-densifolia*. (Figs. 1-4, 6, 8, from material collected by *K. Müller* at the Feldberg, Schwarzwald, Germany; figs. 5, 7, from plants collected at Copper Harbor, Mich., by *W. C. Steere*. Figs. 9-10, 12, from plants collected at Manitoulin

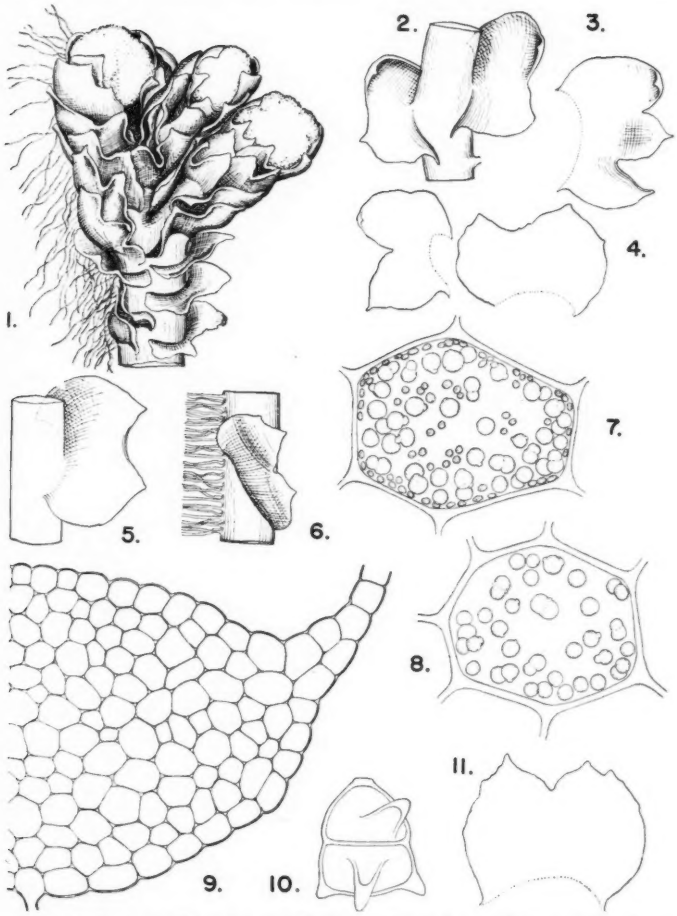


PLATE 10. *Lophozia* (*Massula*) *grandiretis*.—1. Terminal part of plant, mod. *colorata-densifolia*, with gemmae-masses at apex. 2. Part of shoot, dorsal view. 3. Three-lobed leaf. 4. Two bilobed leaves. 5. Leaf, dorsal view, showing insertion. 6. Leaf, lateral view, showing insertion and rhizoids. 7. Cell from leaf-middle, with chloroplasts and oil-bodies. 8. Same, showing oil-bodies only. 9. Cross-section of stem and leaf-base. 10. Gemmae. 11. Leaf. (Figs. 1-6, 9 from material from Big Susie Is., Susie Isls., Cook Co., Minn., *Schuster*. Figs. 7-8, 10-11, from material from Grand Portage, Minn., *Schuster*). Fig. 1, 12×; 2-6, 19×; 7-8, 515×; 9, 130×; 10, 600×; 11, 15×.

Island, Lake Huron, Ontario, by *R. M. Schuster;* fig. 11 from plants collected 5 miles n.e. of Tahaquemon Falls, Luce Co., Mich. by *R. M. Schuster*. Figs. 13-16, from plants collected on Lucille Is., Susie Isls., Cook Co., Minn. by *R. M. Schuster, No. 13657e*). 12, 24×; 13, 13×; 14-15, 16×; 16, 12×.

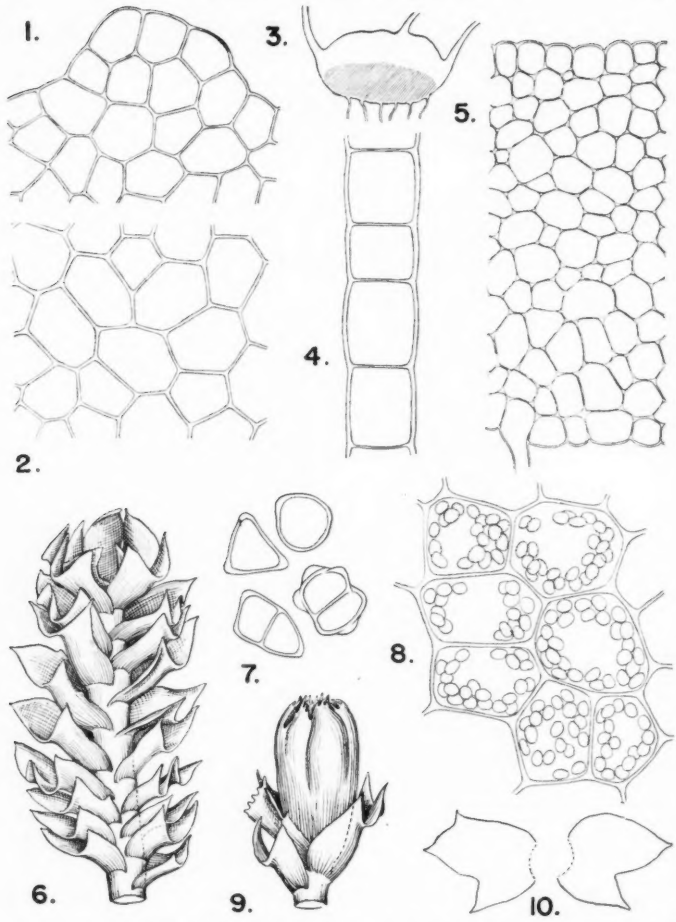


PLATE 11.—*Lophozia* (*Massula*) *grandiretis*. 1. Cells of leaf-lobe. 2. Cells of leaf-middle. 3. Cross-section of stem, the purplish-pigmented region indicated by cross-hatching. 4. Cross-section of leaf. 5. Cross-section of median part of stem. (Figs. 1-5 drawn from material from Big Susie Is., Cook Co., Minn., *Schuster*). Figs. 1-2, 175×; 3, 25×; 4 circa 250×; 5. 150×.

Lophozia (*Massula*) *incisa*. 6. Sterile plant of the var. *inermis* K.M., with collenchymatous cells. 7. Gemmae. 8. Cells of leaf-middle. 9. Perianth of var. *inermis*. 10. Two leaves of var. *inermis*. (Figs. 6, 9, 10 from material from Zealand Falls, near Twin Mt., Coos Co., N. H., *Schuster*. Fig. 7 from Plymouth Bog, Chenango Co., N. Y., *Schuster & Rader*. Fig. 8 from Cascade River, Cook Co., Minn., *Schuster*). Fig. 6, 25×; 7, 425×; 8, 450×; 9, 25×; 10, 18×.

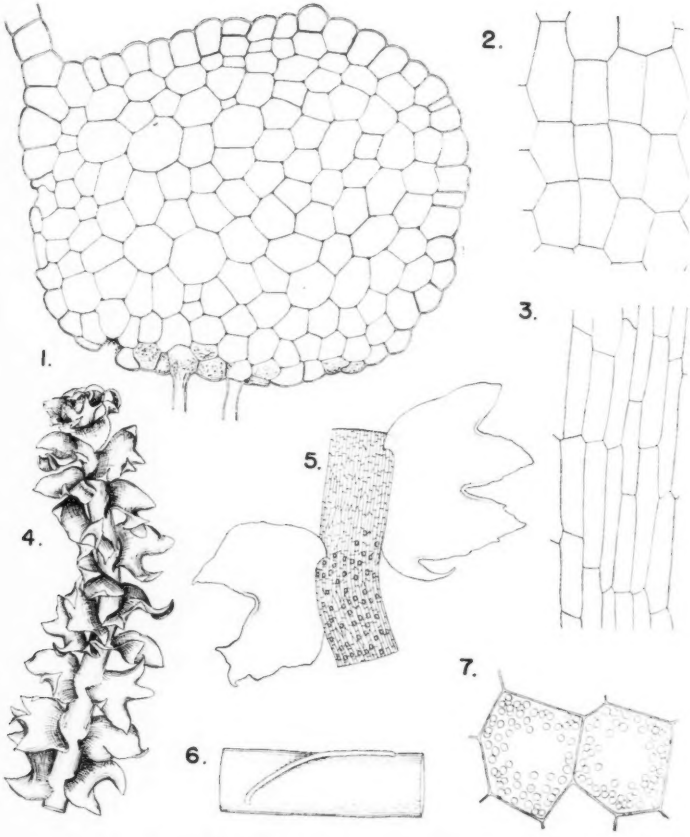


PLATE 12. *Lophozia* (*Massula*) *marchica*.—1. Cross-section of mature stem, showing limited mycorrhizal infection of ventral cortical layers. 2. Basal leaf-cells (same mag. as fig. 3.). 3. Dorsal cortical stem-cells. 4. Gemmiparous shoot. 5. Postical view of shoot sector, the stem-cells drawn in (rhizoid-initials indicated in lower half of figure). 6. Leaf-insertion. 7. Leaf-cells from near leaf-base, showing oil-bodies. (Fig. 1 from material from 8 miles s.w. of Gheen, St. Louis Co., Minn., *Schuster*. Figs. 2-7 from material from Junius Bog, Seneca Co., N. Y., *Schuster*). Fig. 1, 170×; 2-3, 155×; 4, 12×; 5-6, 32×; 7, 380×.

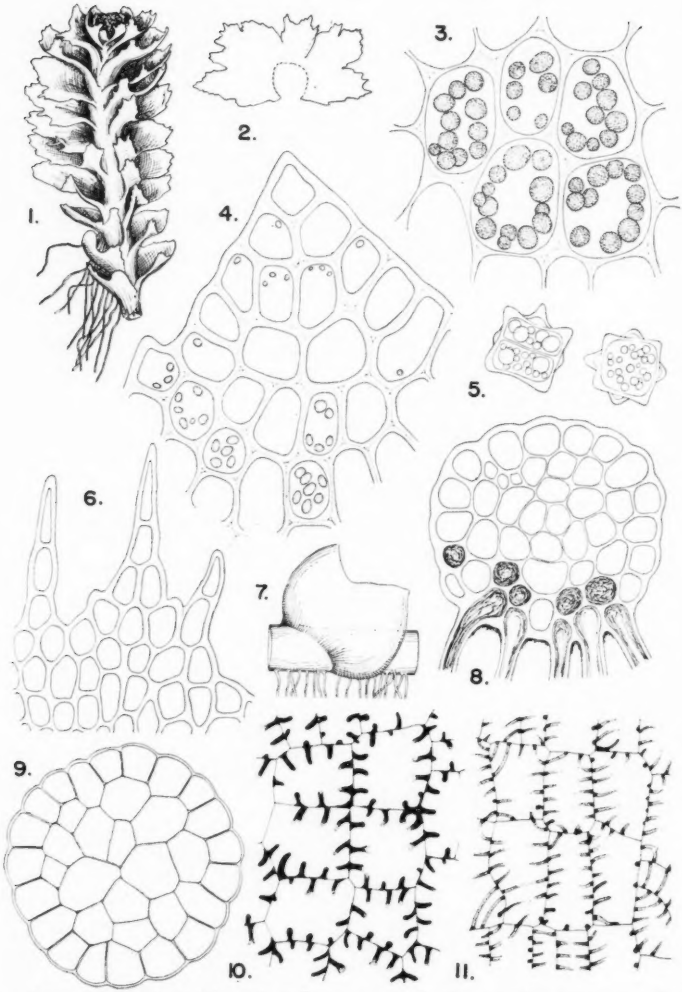


PLATE 13. *Lophozia* (*Isopaches*) *bicrenata*.—1. Sterile, strongly gemmiparous shoot. 2. Involucral bracts and, medially, bracteole. 3. Cells of leaf-middle. 4. Cells of leaf-apex. 5. Gemmae. 6. Perianth-mouth. 7. Leaf, with insertion on stem. 8. Cross-section of stem. 9. Cross-section of seta. 10. Cells of epidermal layer of capsule. 11. Cells of inner layer of capsule. (Fig. 1, Delaware Water Gap, Pa., *Schuster;* Figs. 2, 8-11, Taughannock, near Ithaca, N. Y., *Schuster;* Figs. 3-6, Great Palisade, Lake County, Minn., *Schuster*). Fig. 1, 22×; 2, 15×; 3, 500×; 4, 300×; 5, 440×; 6, 270×; 7, 28×; 8, circa 200×; 9, circa 200×.

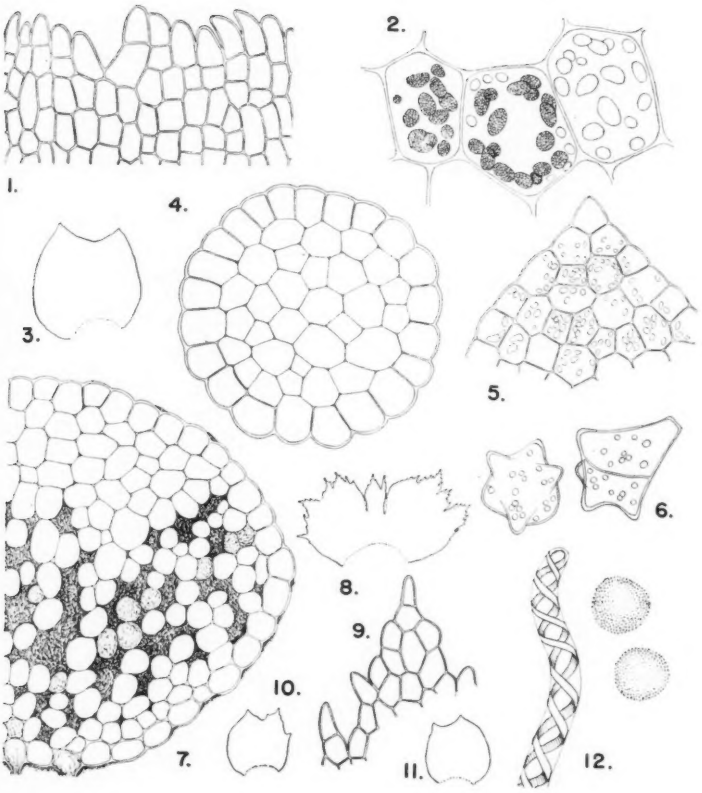


PLATE 14. *Lophozia* (*Dilophozia*) *excisa*.—1. Cells of perianth mouth. 2. Cells of leaf-middle. 3. Leaf. 4. Cross-section of seta. 5. Apex of ventral lobe of leaf in Fig. 3. 6. Gemmae. 7. Cross-section of stem. 8. Ring of perichaetial bracts. 9. Apex of lobe of bracts in fig. 8. 10. Perigonal bract. 11. Leaf. 12. Half of elater and two spores. (Figs. 1-3, 5-6, 10, 12, Grand Portage, Minn., *Schuster;* Figs. 4, 7, South Hill, Ithaca, N. Y., *Schuster* Figs. 8-9, 11, Woodhull, N. Y., *Schuster*). Fig. 1, 200×; 2, 500×; 3, 24×; 4, circa 200×; 5, 210×; 6, 500×; 7, 200×; 8, 12×; 9, circa 200×; 10-11, 12×; 12, 480×.

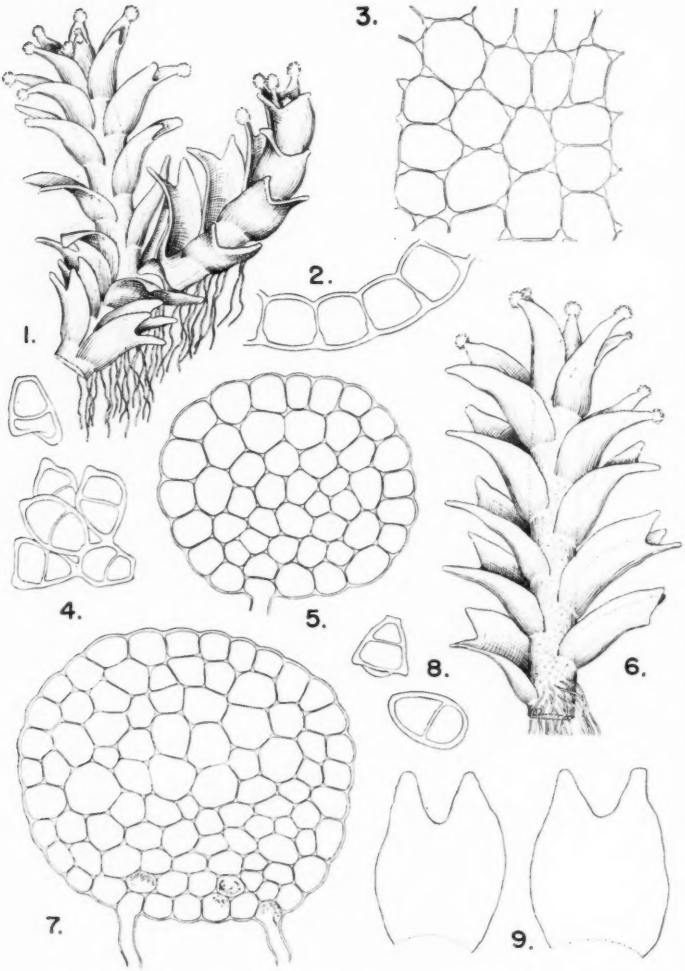


PLATE 15. *Lophozia* (*Dilophozia*) *gracillima*.—1. Gemmiparous plant. 2. Cross-section of part of leaf. 3. Cells of leaf-middle. 4. Gemmae. 5. Cross-section of immature portion of stem. 6. Shoot, ventral view. 7. Cross-section of mature stem, showing slight mycorrhizal infection. 8. Gemmae. 9. Two leaves. (Figs. 1-4, 6-9, from material from Pigeon Point, Cook Co., Minn., *Schuster*, new to North America. Fig. 5, from material from Schwarzwald, Baden, Germany, *K. Müller*). Fig. 1, 20×; 2, 250×; 3, 310×; 4, 520×; 5, 175×; 6, 26×; 7, 190×; 8, 520×; 9, 35×.

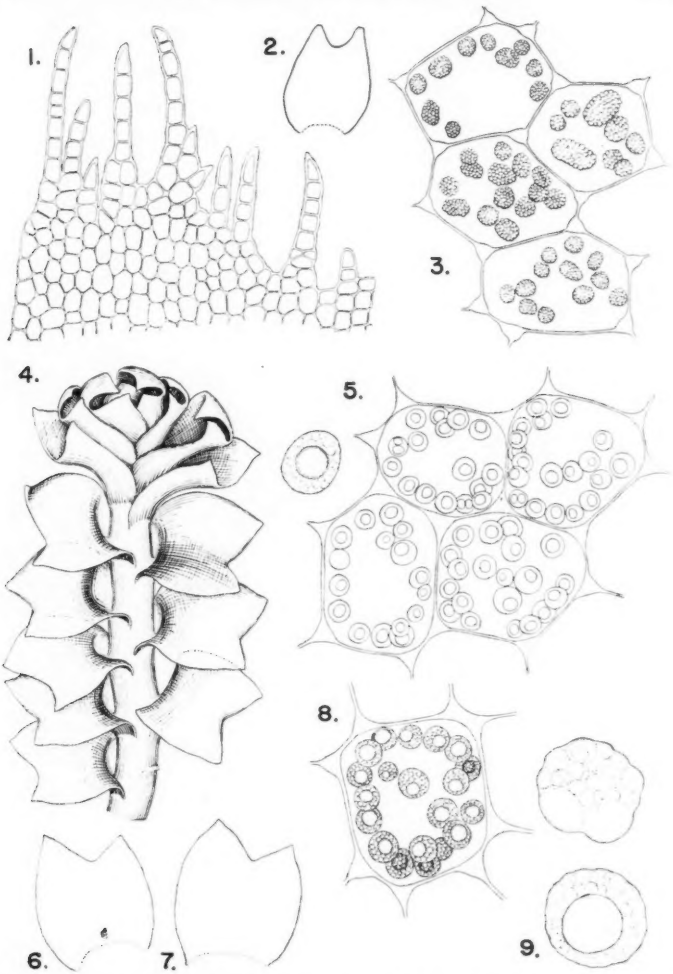


PLATE 16.—*Lophozia* (*Dilophozia*) *longidens*. 1. Cells of perianth-mouth. 2. Leaf. 3. Cells of leaf-middle. (Fig. 1, Belle Rose Is., Susie Isls., Minn. Fig. 2, Raquette Lake, N. Y., *Schuster*. Fig. 3, Island between Lucille and Susie Isls., Susie Isls., Minn., *Schuster*). Fig. 1, circa 170×; 2, 16×; 3, 720×.

Lophozia (*Dilophozia*) *silvicola*. 4. Sterile shoot. 5. Cells of leaf-middle of mod. *leptoderma*, to the left a single oil-body. 6-7. Two leaves. 8. Cells from leaf-middle, showing oil-bodies in detail. 9. Two oil-bodies, the upper in process of disintegration? (Figs. 4-9, Great Palisade Head, 65 miles n. of Duluth, Minn., *Schuster*). Fig. 4, 16×; 5, 720×; 6-7, 24×; 8, 850×; 9, circa 3000×.

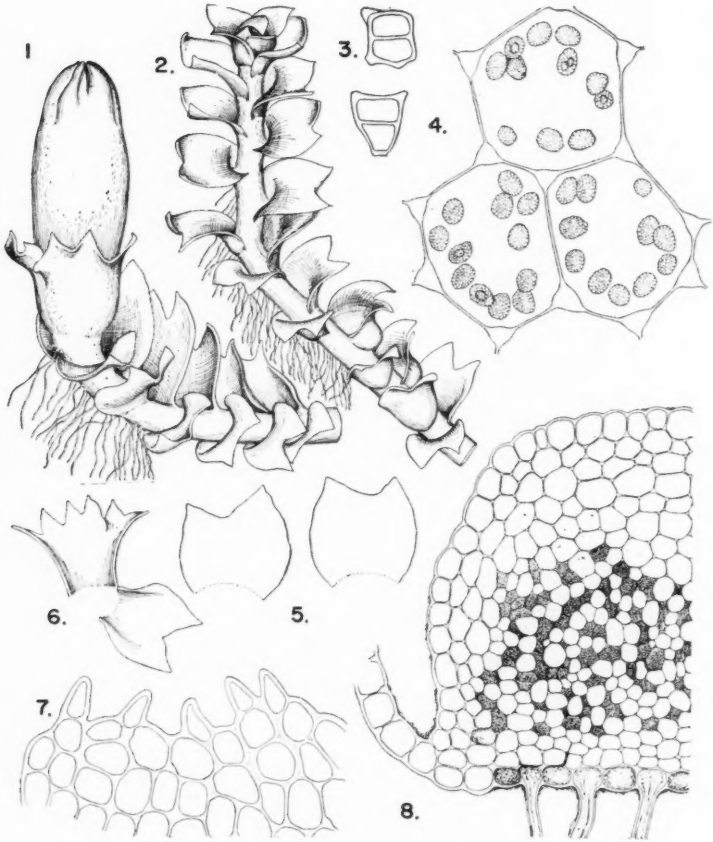


PLATE 17. *Lophozia* (*Dilophozia*) *ventricosa*.—1. Perianth-bearing shoot, of mod. *colorata-mesoderma*, approaching *longiflora*. 2. Shoot with intercalary androecium, from same collection. 3. Gemmae. 4. Cells of leaf-middle, showing oil-bodies. 5. Two leaves. 6. Perichaetial bracts. 7. Cells of perianth-mouth. 8. Cross-section of stem. (Figs. 1-3, 5-8, from material from Pigeon Point, Cook Co., Minn., *Schuster*, of a robust mod. *colorata-mesoderma* approaching var. *longiflora*. Fig. 4, from small island between Lucille and Susie Isls., Susie Isls., Cook Co., Minn., *Schuster*). Figs. 1-2, 14×; 3, 380×; 4, 720×; 5, 14×; 6, 9×; 7, 260×; 8, 150×.

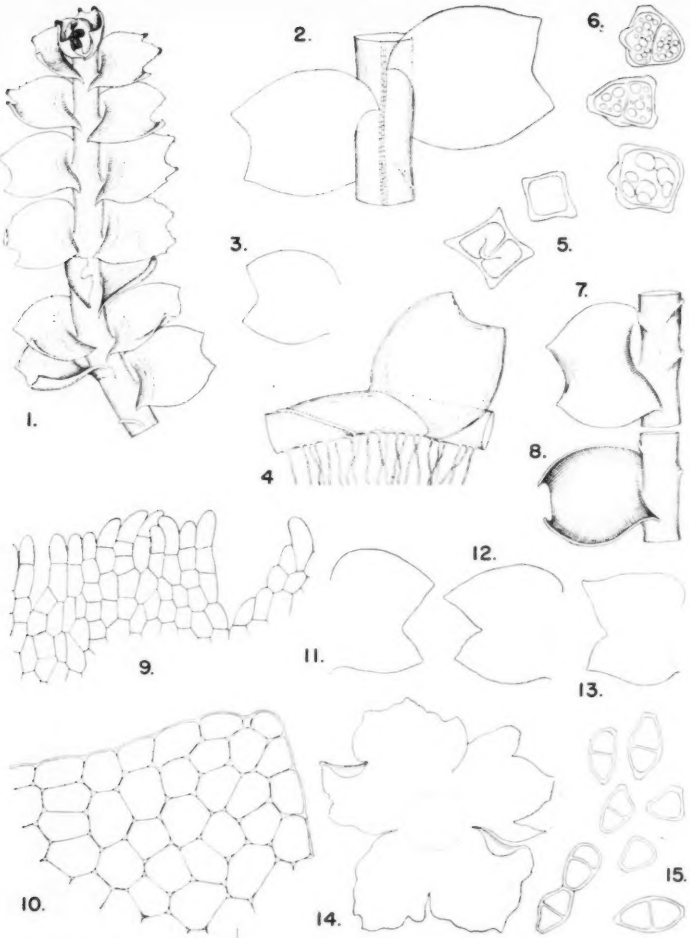


PLATE 18. *Lophozia* (*Dilophozia*) *alpestris*.—1. Gemmiparous shoot. 2. Postical view of portion of shoot, with cells of ventral stem sectors drawn in. 3. Leaf. 4. Part of shoot, lateral view, showing line of leaf-insertion. 5. Gemmae. 6. Gemmae, with oil-bodies drawn in. 7. Leaf and insertion on stem: unusually spreading. 8. Leaf and insertion, from same shoot as Fig. 7, showing normal concavity. *Lophozia* (*Dilophozia*) *latifolia*. 9. Cells of perianth mouth. 10. Cells of apex of leaf-lobe. 11-13. Leaves. 14. Perichaetial bracts, the bracteole to upper right. 15. Gemmae. (Figs. 1-5 drawn from plants collected at Pigeon Point, Cook Co., Minn., *R. M. Schuster;* figs. 6-8 drawn from plants collected at Letchworth Park, Wyoming Co., N. Y., *R. M. Schuster*. Figs. 9-15 drawn from plants collected at Grand Marais, Cook Co., Minn., by *R. M. Schuster*.). Fig. 1, 16×; 2, 24×; 3, 18×; 4, 22×; 5-6, 550×; 7-8, 22×; 9, circa 140×; 10, 210×; 11-14, 16×; 15, 260×

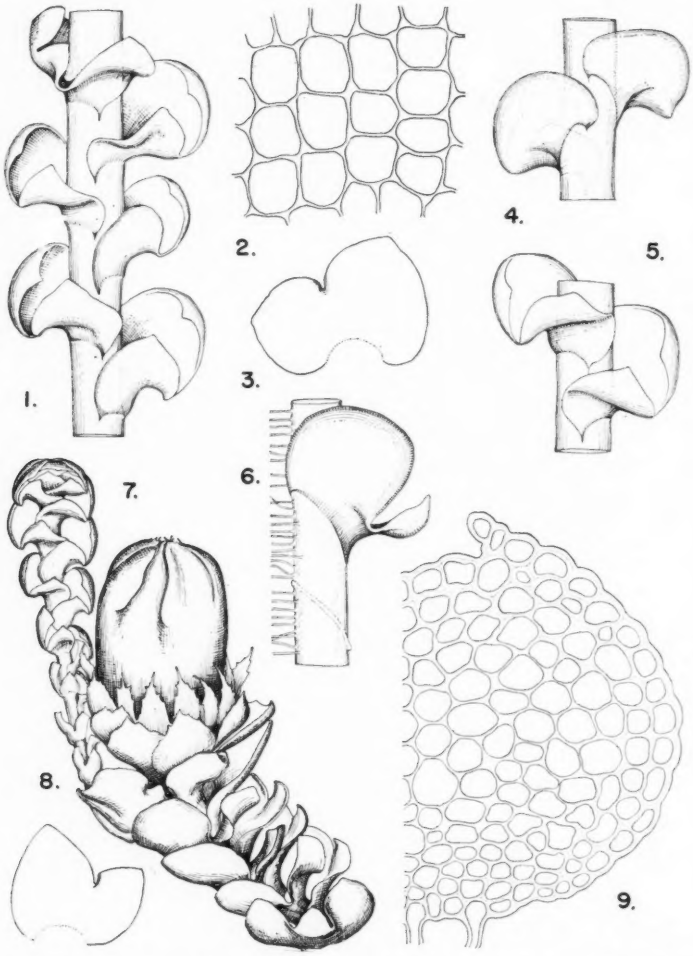


PLATE 19. *Anastrophyllum* (*Eurylobus*) *saxicolus*.—1. Part of shoot, dorsal view. 2. Cells of middle of ventral lobe of mod. *leptoderma*. 3. Large leaf. 4. Part of shoot, postical view. 5. Same, dorsal view. 6. Part of shoot, lateral view, rhizoids drawn in. 7. Plant with immature perianth and subinvolucral innovation. 8. Small leaf. 9. Cross-section of stem. (All drawn from material from Pigeon Point, Cook Co., Minn., *Schuster*, new to the United States). Fig. 1, 23×; 2, 340×; 3, 26; 4-6, 25×; 7, 18×; 8, 26; 9, 240.

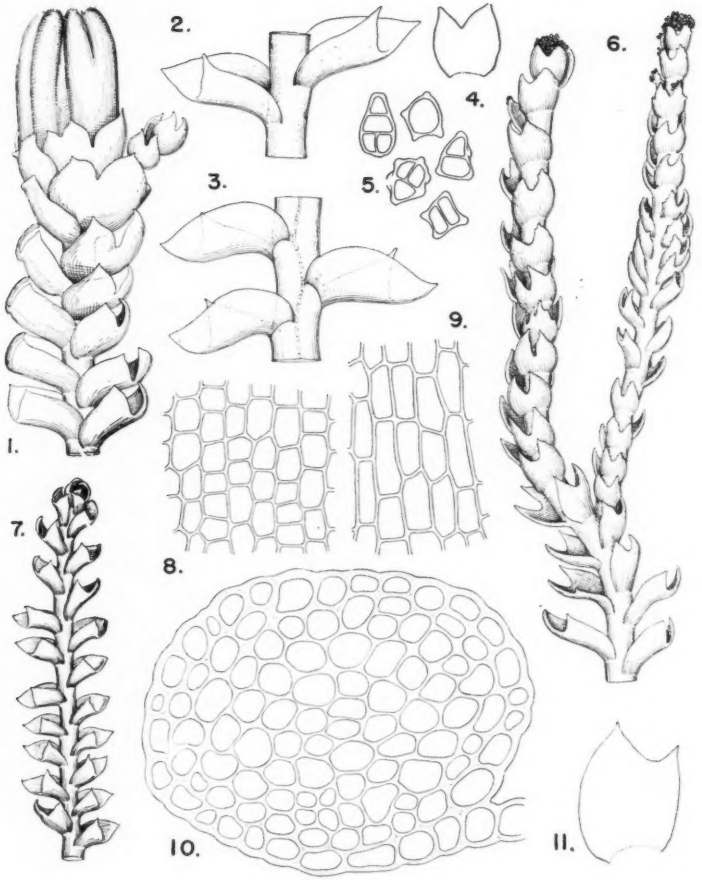


PLATE 20. *Anastrophyllum* (*Sphenolobus*) *minutus*.—1. Fertile plant. 2. Part of shoot, dorsal view. 3. Part of shoot, ventral view, with cells of ventral stem-sectors drawn in. 4. Leaf. 5. Gemmae. 6. Gemmiparous shoot of the mod. *colorata-pachyderma-densifolia*. 7. Sterile shoot. 8. Cells of leaf-base. 9. Epidermal cells of dorsal surface of stem of same plant. 10. Stem cross-section. 11. Leaf. (Fig. 1, Great Palisade, Lake Co., Minn., *Schuster*. Figs. 2-3, 8-11, small island between Lucille and Susie Isls., Cook Co., Minn., *Schuster*. Figs. 4, 7, Blue Mt., N. Y., *Schuster*. Figs. 5-6, Olean Rock City, Cattaraugus Co., N. Y., *Schuster & Rader*). Fig. 1, 20×; 2, 40×; 3, 33×; 4, 25×; 5, 280×; 6, 45×; 7, 18×; 8-9, 240×; 10, 360×; 11, 45.

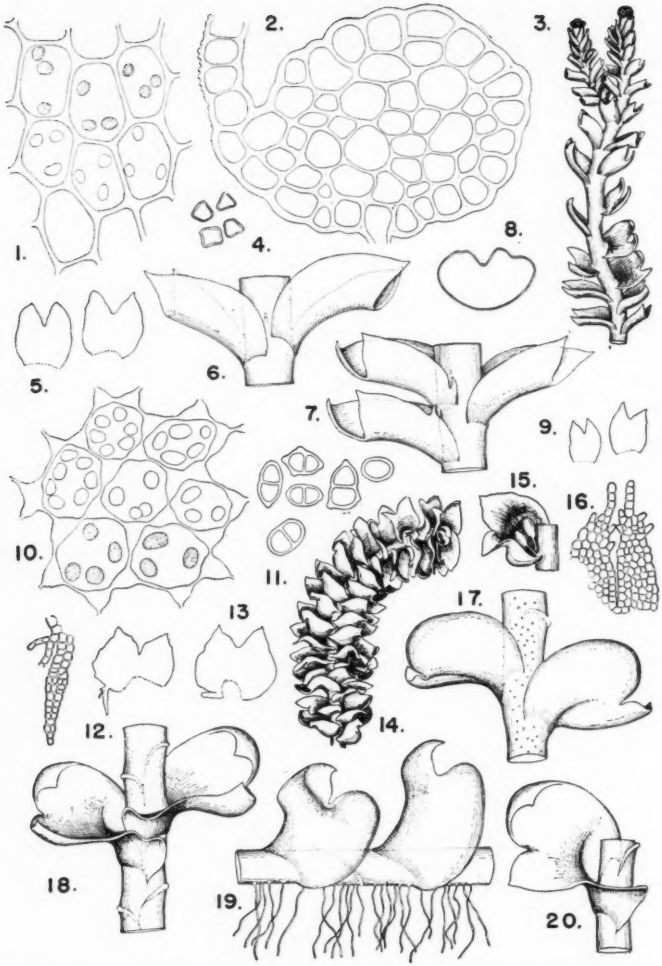


PLATE 21.—*Anastrophyllum* (*Crossocalyx*) *hellerianus*. 1. Cells of leaf-middle, with oil-bodies drawn in. 2. Stem cross-section. 3. Gemmiparous shoot, with slight dimorphism. 4. Gemmae. 5. Two leaves from middle of plant in fig. 3. 6. Part of shoot, fertile plant, postical view, note stalked slime papilla. 7. Same dorsal view. 8. Perianth cross-section (antical side on top). 9. Two leaves (from near apex of gemmiparous shoot in fig. 3). (Figs. 1-2, 6-8, Cascade River Ravine, Cook Co., Minn., *Schuster;* Figs. 3, 5, 9, Briggs Gully, Ontario Co., N. Y., *Schuster;* Fig. 4, Mountain north of Mt. MacIntyre, N. Y., *Schuster & Matthysse*). Fig. 1, 580×; 2, 250×; 3, 20×; 4, 250×; 5, 25×; 6-7, 47×; 8, 30×; 9, 25×.

Anastrophyllum (*Euanastrophyllum*) *michauxii*. 10. Cells of leaf-middle, with oil-bodies drawn in. 11. Gemmae. 12. Male bract, with basal, ciliate tooth of antical margin more highly magnified (left). 13. Normal leaf, but with basal tooth of antical margin. 14. Male plant, showing androecium and part of an older androecium (at base). 15.

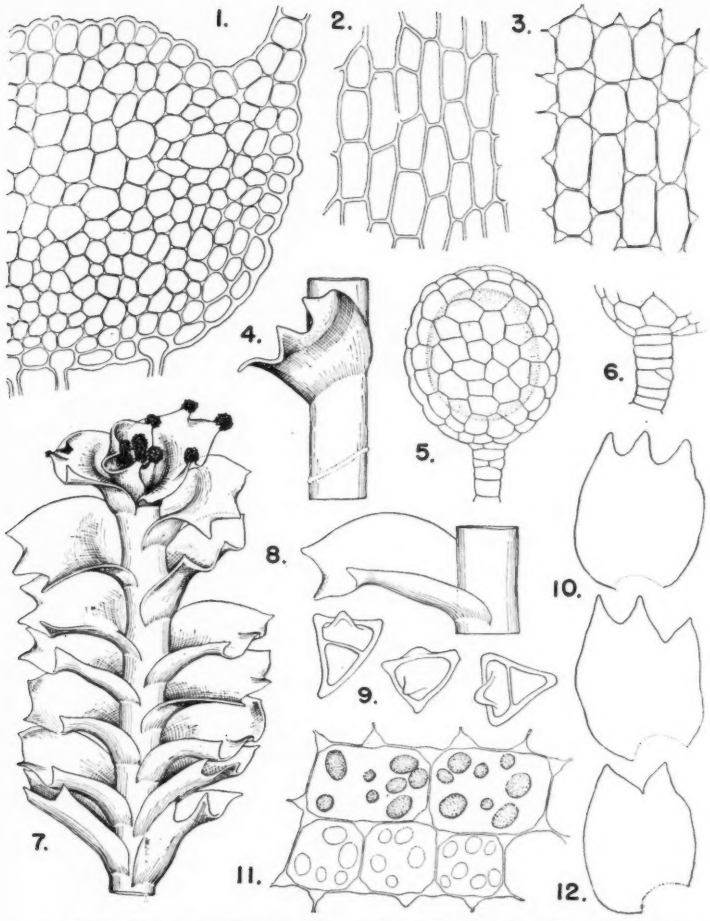


PLATE 22. *Tritomaria* (*Eutritomaria*) *scitula*.—1. Cross-section of stem (mycorrhiza omitted). 2. Dorsal cortical stem cells of mod. *densifolia*. 3. Basal leaf cells (same magnification as fig. 2). 4. Lateral view of section of shoot, rhizoids omitted. 5. Antheridium. 6. Stalk of antheridium. 7. Gemmiparous shoot. 8. Leaf, dorsal view. 9. Gemmae. 10 Two leaves. 11. Cells from leaf-middle, showing oil-bodies. 12. Bilobed leaf (from same shoot as leaves in fig. 10). (All drawn from *Schuster* 11967, small island between Lucille and Susie Isls., Susie Isls., Cook Co., Minn.). Fig. 1, 170×; 2-3, 200×; 4, 28×; 5, 145×; 6, 220×; 7, 21×; 8, 28×; 9, 600×; 10, 28×; 11, 450×; 12, 28×.

Male bract, the antical lobe somewhat bent away to show antheridia. 16. Part of perianth-mouth. 17. Part of shoot, postical view (rhizoid-initials indicated as circles). 18. Same, dorsal view. 19. Same, lateral view. 20. Leaf, dorsal view, showing insertion. (Fig. 10, Cascade River Ravine, Minn., *Schuster;* Fig. 11, Rock City, Cattaraugus Co., N. Y., *Schuster & Rader;* Figs. 12-16, North of Raquette Lake, N. Y., *Schuster;* Figs. 17-20, Big Susie Is., Susie Isls., Cook Co., Minn., *Schuster*). Fig. 10, 400×; 11, 250×; 12-13, 14×; 14, 8×; 15, 14×; 16, circa 60×; 17, 30×; 18-19, 25×; 20, 20×.

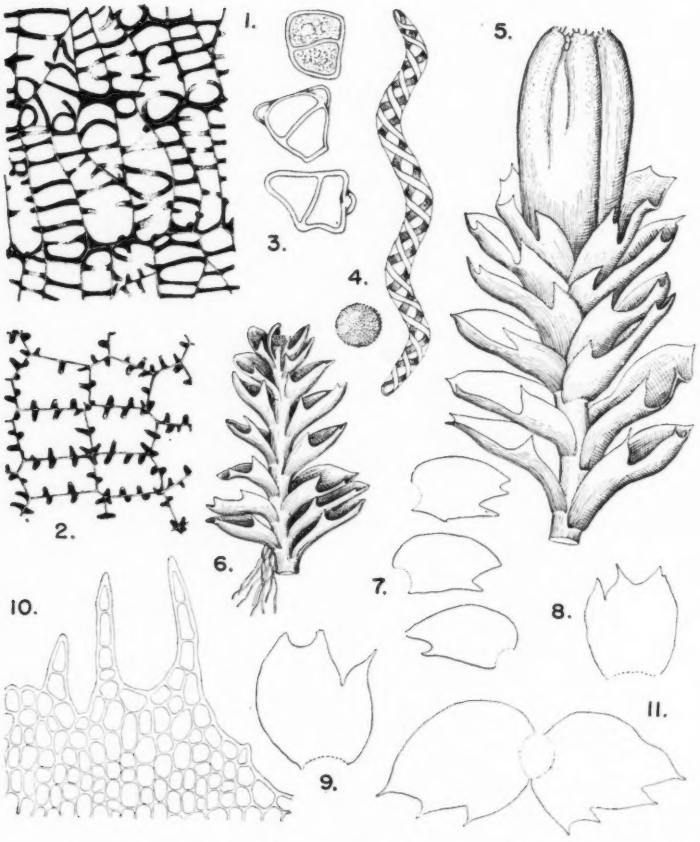


PLATE 23. *Tritomaria* (*Eutritomaria*) *exsectiformis*.—1. Inner layer of capsule-wall. 2. Outer cell-layer of capsule wall. 3. Gemmae. 4. Spore and elater (from same capsule as figs. 1-2). 5. Fertile plant. 6. Sterile, gemmiparous shoot (rhizoids indicated at base only). 7. Three leaves (somewhat atypical). 8-9. Male bracts. 10. Cells of perianth-mouth. 11. Perichaetial ring of bracts. Figs. 1-5, 8-11, Big Susie Is., Susie Isls., Cook Co., Minn., *Schuster;* Fig. 6, Delaware Water Gap, Pa., *Schuster*. Fig. 7, Rock City, Cattaraugus Co., N. Y., *Schuster & Rader*). Figs. 1-2, 290×; 3, 600×; 4, 550×; 5, 20×; 6, 16×; 7-9, 18×; 10, 175×; 11, 18×.

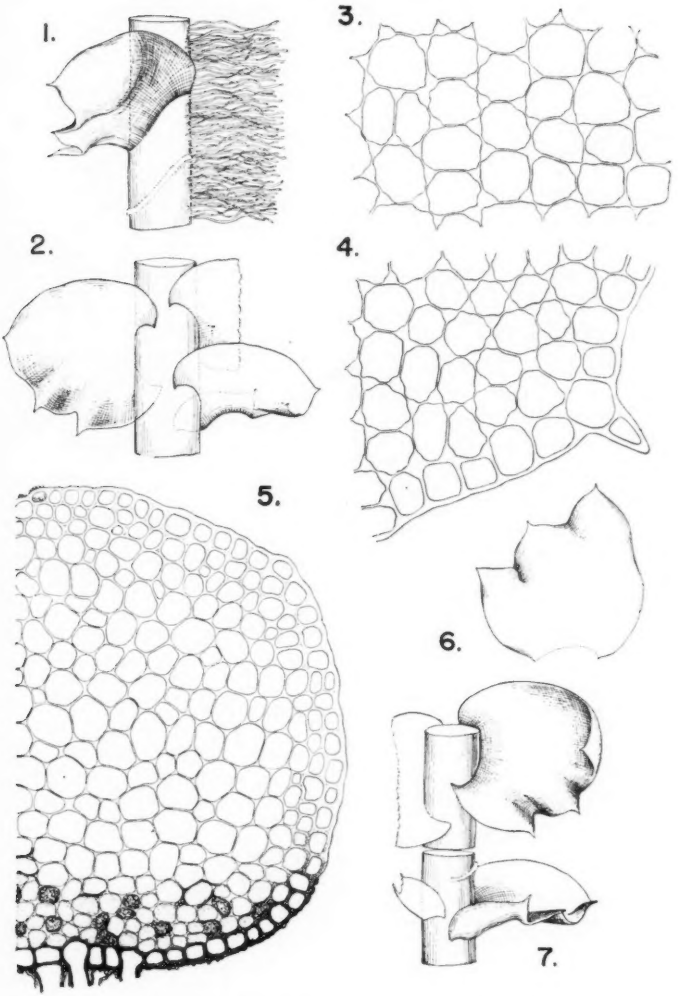


PLATE 24. *Tritomaria* (*Trilophozia*) *quinquedentata*.—1. Part of shoot, lateral view. 2. Same, postical view (rhizoids omitted). 3. Cells of leaf-middle. 4. Cells of apex of ventral lobe. 5. Stem cross-section (brownish pigmented area indicated by stippling; mycorrhiza by lines). 6. Leaf, almost flattened out. 7. Part of shoot, dorsal view; above, with spreading leaves, below, with canaliculate leaves. (All drawn from material from Gunflint Lake, Minn.). Figs. 1-2, 23×; 3-4, 320×; 5, circa 180×; 6, 25×; 7, 23×.

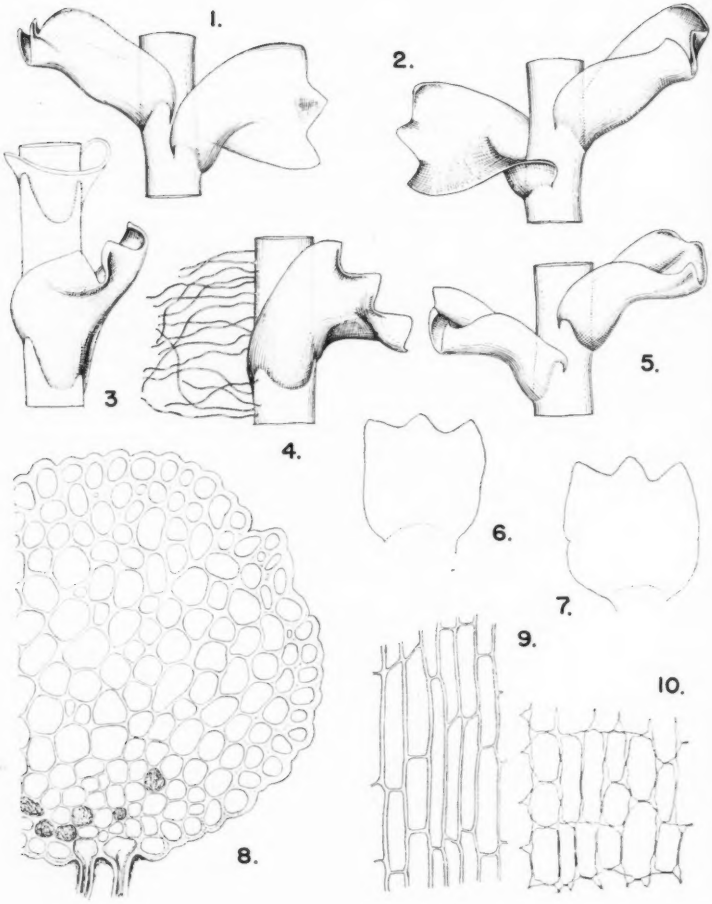


PLATE 25. *Saccobasis polita*.—1. Postical view of part of shoot (rhizoids omitted). 2. Same, dorsal view. 3. Lateral view of part of shoot (rhizoids omitted). 4. Same, with rhizoids drawn in. 5. Dorsal view of lax-leaved plant. 6-7. Two leaves, flattened. 8. Stem-section (pigmented area stippled; mycorrhiza indicated by lines). 9. Cells of dorsal surface of stem. 10. Cells of leaf-base (same magnif. as fig. 9). (All drawn from material collected by *Loitlesberger* in Austria). Figs. 1-2, 18×; 3-4, 21×; 5, 16×; 6-7, 13×; 8, 160×; 9-10, 110×.

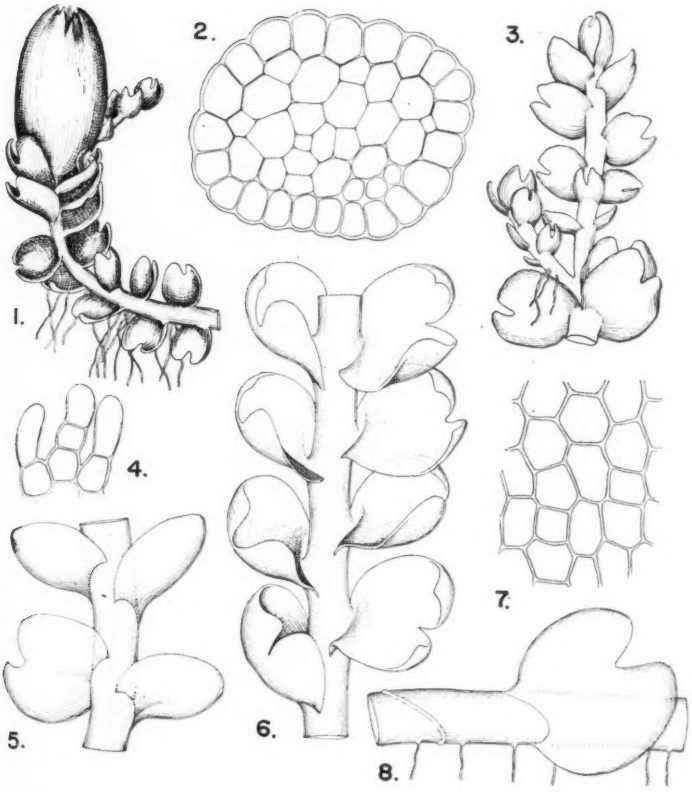


PLATE 26. *Gymnocolea inflata*.—1. Plant with sterile perianth and postical innovation. 2. Stem-section of moderate-sized plant. 3. Postical view of apex of fertile plant that bore caducous perianth, showing innovations and rhizoids. 4. Underleaf, from fertile plant. 5. Postical view of part of robust shoot. 6. Same, antical view. 7. Ventral cortical stem cells. 8. Lateral view of part of shoot, showing rhizoids. (Figs. 1-2, 5-6, 8, Taughannock Ravine near Ithaca, N. Y., *Schuster;* Figs. 3-4, 7, Gunflint Lake, Cook Co., Minn., *Schuster*). Fig. 1, 16×; 2, 200×; 3, 18×; 5-6, 30×; 7, 240×; 8, 45×.

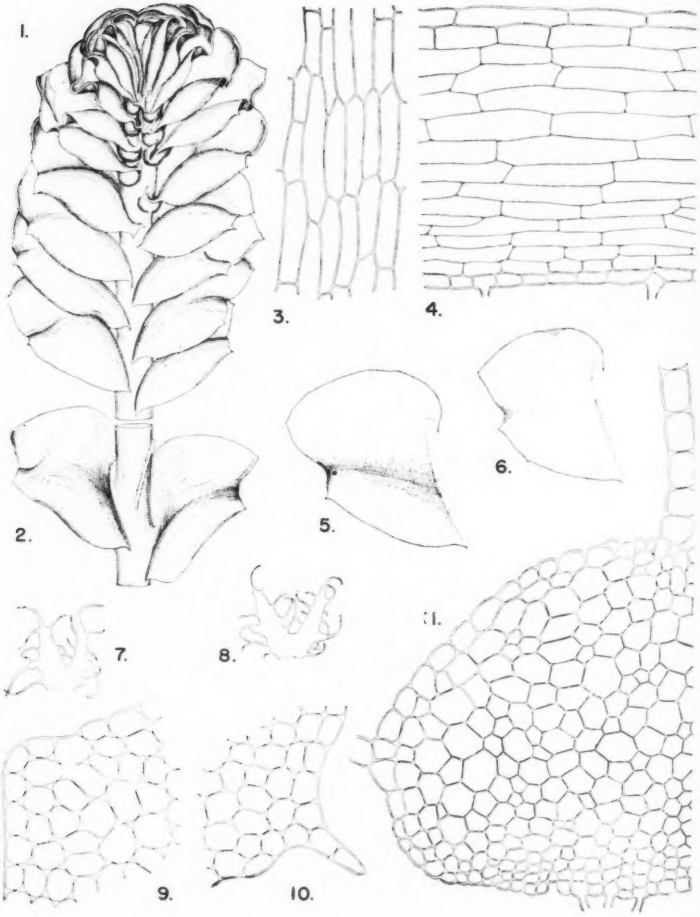


PLATE 27. *Mesoptychia sahlbergii*.—1. Apex of male plant. 2. Lower part of same plant, showing normal leaves. 3. Cells of dorsal stem surface. 4. Longitudinal median section of stem. 5, 6. Leaves. 7, 8. Underleaves. 9. Cells of apex of ventral lobe. 10. Cells of apex of dorsal lobe (of same leaf as in Fig. 9). 11. Cross-section of stem (intercepting two leaf-bases). (Figs. 1-11 all drawn from material collected on the Lena River, Siberia.). Figs. 1-2, 9×; 3, 145×; 4, 130×; 5-6, 10×; 7-8, 16×; 9-10, 160×; 11, 145×.

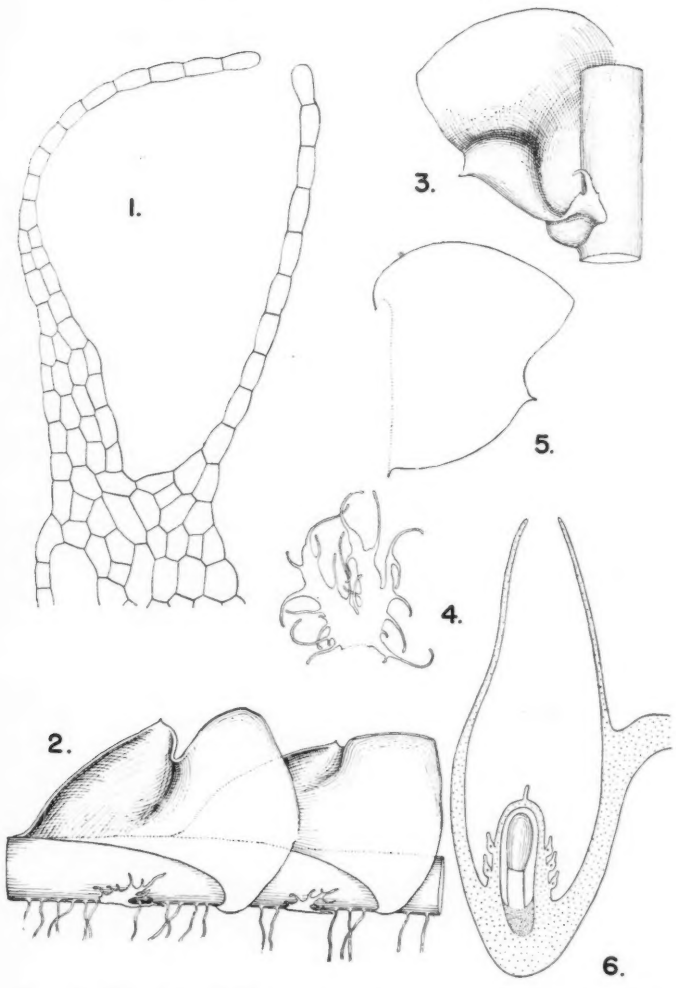


PLATE 28. *Mesoptychia sahlbergii*.—1. Lobe of underleaf shown in Fig. 4. 2. Part of shoot with suberect, dorsally connivent leaves. 3. Male bract. 4. Underleaf, of sterile shoot. 5. Normal leaf. 6. Perigynium and apex of female plant (after K. Müller). Figs. 1-5 drawn from material collected on the Lena River, Siberia.). Fig. 1, 140×; 2-3, 14×; 4, 25×; 5, 15×.

Ficus in Florida—III. Asiatic Species

Mary F. Barrett
Bloomfield, New Jersey

Introduction

This series of studies, like previous ones in this magazine* and elsewhere,** is intended to bring up to date the synonymy and descriptions of several species of *Ficus* cultivated in Florida, and likely to be increased by post-war botanical expeditions to tropical and subtropical countries.

The present grouping is of a few species native to one or more of the following regions: India, Malaya, Indo-China, and China; although often found more widely distributed.

Living trees of these species were studied by me in southern Florida during the years 1936, 1937, 1938, and 1949. Some of the public places where they were seen in 1949 are listed in this text under the following abbreviations: CF (Chapman Field, a Plant Introduction Station of the U.S. Dept. of Agriculture, south of Coconut Grove), DCN (Dade Co. Nurseries, Red Road, South Miami), Ed. (Edison Place, Fort Myers), FM (Fort Myers), FTG (Fairchild Tropical Garden, Coconut Grove), KW (Key West), MCC (Miami City Cemetery), Mi. (Miami), MK (McKee Jungle Gardens, Vero Beach), PG (Punta Gorda), RPN (Royal Palm Nurseries, Oneco), Sar. (Sarasota), VB (Vero Beach), W (Woodlawn Park & Mausoleum, Miami).

Library work has been done at the New York Botanical Garden (NYBG), and herbarium specimens have been examined there and at the Arnold Arboretum (AA), Jamaica Plain, Mass.; the Bailey Hortorium (BH), Ithaca, New York; the United States Museum (US), Washington, D. C.; and the University of Florida (UF), Gainesville, Florida. Specimens bearing the letters U.S.P.I. or P.I. are those from plants cultivated and sometimes distributed from the United States Plant Introduction division.

My thanks are extended to all those who made these facilities available to me, including those mentioned in my previous studies, and also Dr. Liberty Hyde Bailey of Ithaca, Dr. H. W. Rickett of the New York Botanical Garden, and the present superintendents of the various botanical gardens and nurseries.

In the following text species which include more than one previously designated form or variety have had the original form named var. *typica* by me. Aside from these the only new name published has been the combination *F. mysorensis* var. *dasycarpa* (Miq.), which replaces the non-valid var. *pubescens* King. *F. benjamina* var. *nuda* (Miq.) is here suggested, but not published.

* *Ficus* in Florida—I. Australian Species. Amer. Midl. Nat. 36: 412-430. 1946. [1947]. *Ficus* in Florida—II. African Species. *Ibid.* 39: 188-219. 1948.

** In Bull. Torrey Bot. Club: *F. altissima* Blume and *F. bengalensis* L. 72: 394-398. 1945. *F. tsjahela* Burm. f. 73: 86-90. 1946. *F. racemosa* L. (*F. glomerata* Roxb.) 73: 312-325. 1946. *F. retusa* 76: 53-64. 1949.

Correct dates of publication and authors have been emphasized especially in the species *elastica, lacor,* and *mysorensis.* Flower descriptions are derived mostly from King and Gagnepain.

In order to shorten the bibliography at the end of the series references which apply to only one species usually are stated in full in the text.

FICUS BENJAMINA L. Mant. 129. 1767

The trees usually called *Ficus benjamina* in Florida are desirable for lawn and street planting because of their habit and the density of their somewhat striate-leaved foliage. Their drooping branches and twigs make graceful umbrella-like shapes on lawns, or, after the removal of some of the lower parts, create tree-tunnels along streets.

F. benjamina is recommended for southern Florida by Mowry (1938) 50. pl. 42; Nehrling (1944) 1: 328; Sturrock & Menninger (1946) various pp.; Gaines R. Wilson (1938) 64, 65; and other writers. It is popularly known as Benjamin Tree, Java Fig, Java Willow, and Weeping Laurel.

This easily recognized small-leaved species consists of several related forms whose differences, less prominent than their similarities, have caused botanists to make separate species out of what, to a layman, appears but one. In order to present the evidence for and against such separations it is necessary to designate the standard of comparison, the original *F. benjamina* (if that can be agreed upon) as var. *typica.* Two other similar forms seen in Florida originally were named *F. waringiana* and *F. nuda. F. benjamina* var. *comosa* has been doubtfully reported from this state, but var. *haematocarpa* probably is absent or undifferentiated from one of the other forms.

In the following synonymy of *F. benjamina* var. *typica* have been included certain names which eventually may prove to belong elsewhere. They have been given places in the synonymy because they have been accepted by authorities as belonging to the whole species *benjamina.* No valuable specimens of them were seen by me, and their descriptions were too meagre for their final allocation.

Ficus benjamina var. typica M. F. Barrett, var. nov.

[*Itty-alu* Rheede, Hort. Mal. 1: 45. pl. 26. 1678]. [*Ficus malabarensis, folio densiusculo nitente, fructu parvo, rotundo, coronato* Syen in Rheede, *Ibid.* 1: 46]. [*Ficus arbor densioribus foliis parvis integris ambonensis* Pluk. Phyt. pl. 243, f. 4. 1692. Alm. 145. 1696]. [*Varinga parvifolia alta* Rumph. Herb. Amboin. 3: 139. pl. 90. 1743]. [*Varinga parvifolia humilis* Rumph. *Ibid.* 3: 139]. *Ficus beniamina* L. Mant. *Ficus indica* João Loureiro, Flora cochinchinensis, edition 1, 2: 665. 1790. *F. picta* Noronha, Verh. Batav. Gen. 5, ed. 1, Art. 4: 15. 1790. *Nomen nudum. F. pyrifolia* Salisb. Prod. 16. 1796. Not Boerl, Burman f., Desfontaines, Lamarck, or F.-Villar. *F. striata* Roth ap. Roem. & Schult. Syst. Veg. 1: 507. 1817. *F. nitida* Heyne ex Roth, Nov. Pl. Sp. 387. 1821. As synonym. *F. pendula* Link, Enum. Hort. Berol. 2: 450. 1822. *F. dictyophylla* Wall. Cat. no. 4502 A, B, D. 1831. *Nomen nudum.* As synonym. *F. haematocarpa* Blume ex Decne. Nouv. Ann. Mus. Paris 3: 494. 1834. *F. neglecta* Blume ex Decne. *Ibid. Urostigma benjamineum* (L.) Miq. Hook. Lond. Jour. Bot. 6: 583. 1847. *U. haematocarpum* Blume ap. Decne.) Miq. *Ibid.* 6: 584. *U. neglectum* (Blume ap. Decne.) Miq. Fl. Ind. Batav. 1[2]: 347. 1859. *F. beniamina* β *haematocarpa* (Blume ap. Decne.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 288. 1867. *F. benjamina* proper Kurz, For. Fl. Brit.

Burma 2: 446. 1877. Incorrect form. *F. comosa* Haines, Bot. Bihar & Orissa pt. 5: 828. 1924. In part. *F. waringiana* Hort. ex G. R. Wilson, Proc. Fla. Hort. Soc. 1937: 64 1938. *Nomen nudum.*

A glabrous (except for stipules and basal bracts of the receptacle) tree becoming 25 or 30, or rarely 50 m. high in its native home; sometimes starting as an epiphyte which destroys a supporting tree by embracing it with aerial roots, and then by these and more roots from the base of its lower branches forms a new trunk; main trunk thick, grooved and ridged if made by aerial roots, otherwise light-colored, fissured showing inner darker bark; props, buttresses, and spreading over-ground roots from base of trunk; sometimes secondary trunks from aerial roots from the branches, forming a banyan type of tree; crown large, dense; branches long, drooping, bearing a few aerial roots which do not always reach the ground; twigs numerous, slender, hanging, light-colored, sometimes scurfy; lenticels becoming brownish, elongated horizontally; terminal buds narrow-conical, 1-2 cm. long (shorter in form *haematocarpa*), green, becoming brown, glabrescent, easily broken off; petioles slender, 1-3 cm. long, yellow-green; blades thin, but stiff when dry, ovate or rarely elliptic; 6-14 x 3-6 5 cm. (examples: 8.5 x 3.5, 10 x 4.5, 11 x 5.5 cm.); apex narrowed, sometimes rounded, then rather gradually, but sometimes abruptly, acuminate; acumen rather thick at base, narrowing to an obtuse tip, about 1-1.5 cm. long, often bent to one side; base slightly narrowed, rounded or sometimes a little decurrent on petiole; margin entire, with a cartilaginous-like rim; upper surface dark green, shining, slightly depressed, when dry, along midrib, not, or only faintly, papillate; under surface paler, papillae almost or quite invisible; midrib continuous to apex, light-colored, prominent, 1-2 mm. wide at base; basal veins faint, sometimes indistinguishable from the lateral veins, forming with them a shallow-indented marginal vein whose indentations are 1-2 mm. from the margin; lateral veins about 8-15 sets in body of blade, upper angle at midrib 60°-70°, appearing more numerous because of several rows of reticular spaces which are elongated horizontally and whose apical and basal walls give an effect of striations parallel to the lateral veins which enclose that section of the reticulum; no checkered background; receptacles axillary, paired at first, sessile, ovoid-globose, typically 0.8-1.3 cm. in height, greenish to yellow, then to reddish, surface when dry wrinkled but not corrugated; apical bracts 4-5, tiny, sometimes erect; basal bracts 3, ovate or angled, united at base; each 1.5-2 mm. long; flowers (according to King or Gagnepain) male, gall, and female in same receptacle; male flowers few, pedicellate, perianth of two large flat parts, one stamen, anther almost sessile; gall flowers mostly pedicelled, 3 or 4 long-spatulate perianth parts, ovary ovoid, smooth; female flowers sessile or short-pedicelled, about 2.5 mm. long, accompanied by linear or oblong bracts, perianth parts 3, obovate or oblong, obtuse, about 1 mm. long, ovary short-attenuate on the stipe, humped at summit, about 0 75 mm. long, style a little lateral, about 1.2 mm. long, stigmatic and papillose over 0.6 mm., achene subreniform, about 1.5 x 1 mm., sessile.

Type: India (according to Linnaeus).

Distribution: Native to Burma, Malaya, Indo-China, southwestern China, Philippines and other southwest Pacific Islands, perhaps to northeastern India. Widely planted elsewhere in India, and in Australia and other continents.

Common name: Benjamin Fig.

Specimens: Trees examined at MK, CF, FTG, MCC, and various other places in Vero Beach and Miami. Herbarium specimens seen at NYBG, AA, UF, BH. A leaf-bearing twig collected by J. D. Hooker at Sikkim, northeastern India, had been noted by Dr. E. D. Merrill as "true *F. benjamina* L." A typical specimen from Hainan is *S. K. Lau* 97. Another: *U.S.P.I.* no. 124232.

Descriptions: In most texts on Indian botany.

Illustrations in addition to those in the synonymy: King, (1887-1888) 1: pl. 52 A, 83[b]; Koorders & Valeton (1916) pl. 735.

SYNONYMY OF VAR. TYPICA

F. benjamina L.—The specific name in Mantissa (1767) is spelled with an *i* instead of the alternate *j*. The text includes the distinguishing characters of slender branches, ovate blades, acuminate leaf-apex, and striate veining. The habit of the tree is called that of *Pyrus:* an indefinite comparison, since Linnaeus (1753) had designated pear, apple, and quince as the three species in that genus.* The distribution was stated as India. References were cited to Rheede and to Rumphius, although the title given by Rumphius was miscalled *Varinga parviflora.* In Mantissa (1771) 519 Linnaeus added a reference to Plukenet.

According to Savage (1945) 185 the Linnean herbarium contained no specimen labeled *F. benjamina,* although J. E. Smith thought that *F. lactea Waringi,* from its description, belonged to that species. [Blume (1825) 456 cited *Waringi* as a Javan name for *F. benjamina.* See also the comment on a later page on *Varinga parvifolia*]. There is no evidence in the earlier writings of Linnaeus that he had seen the plant which he named *F. benjamina,* although L. (1759) 4: 124 states that *Varinga parvifolia* Rumph. is a *Ficus.*

Perhaps because of the four rather doubtful pre-Linnean references King (1887-1888) 1: 43-44 thought that Linnaeus might have had had *F. retusa* var. *nitida* (Thunb.) Miq. in mind when describing *F. benjamina,* and Merrill (1917) 195 believed that more than one species was included in the Linnean text. But Linnaeus described *F. retusa* on the same page in Mantissa with *F. benjamina,* saying that the leaves were oblong or cuneiform-obovate and very obtuse. These characters apply much better to both var. *typica* and var. *nitida* of *F. retusa* than they do to the distinctly acuminate-leaved *F. benjamina,* and constitute a good argument that Linnaeus was able to differentiate the two species. However, the confusion which has existed between *F. benjamina* and other forms is partly evidenced by the list of homonyms which concludes the study of this species.

Itty-Alu Rheede.—This name was generally accepted as a synonym by botanists and compilers of the early 19th century, but has been excluded by King, Forbes & Hemsley (1899) 26: 458, Koorders & Valeton (1906) 11: 118-120, and others.

The principal characters of *Itty-Alu* which are incongruous with *F. benjamina* are the very short acumen of the leaves and the peduncled figs crowned with apparently united apical bracts. The first character is found in *F. retusa.* The figs are unlike those of both *F. retusa* and *F. benjamina.* Characters

* See L. H. Bailey in *Gentes Herbarium* 8, fasc. I: 40. 1949.

resembling those of *F. benjamina* are the striate veining of the leaf, the lack of very distinct basal veins, and the larger leaf than in *F. retusa* (so stated under *Itti-arealou* Rheede). The prominent midrib and the marginal vein are emphasized. The habit, with its many spreading branches, aerial roots dangling from them, and thick trunk with its prop roots stretching over the ground, seems to characterize the species as *F. benjamina*. It is significant that secondary trunks are not mentioned, that the descriptive polynomial appended to the text by Arnold Syen, the editor, omitted the peduncle of the fig, and that Linnaeus excluded the receptacle altogether.

The conclusion here reached is that Rheede's species probably represents one form of *F. benjamina*. The same blade-shape is found in some specimens, and the acuminate apex seems to become worn down and blunted in old leaves.

Plukenet's polynomial.—Plukenet's plate and text indicate leaves like those of *F. benjamina*, cite references to a Jamaican species (not a true synonym) and to *Itty-Alu*, and remark that this *Ficus* propagates by air roots from the branches. This statement and the location of the tree in Amboina suggest Rumphius's *Varinga parvifolia humilis*, which may be f. *haematocarpa*. If the discrepancy between the dates of Plukenet's works and the text by Rumphius seems too great it must be remembered that the original manuscript of *Herbarium Amboinense* was lost at sea as it was on its way to publication in Holland, that the plates and text had to be re-made, and that the volumes remained unprinted in Holland for several years. It is quite possible that specimens of *Varinga parvifolia* were sent to the English gardens of which Plukenet was director, even before a name was given them by Rumphius.

Varinga parvifolia Rumph.—*Varinga* was the Latin form of the native name *Waringin*, which still is applied in Java and elsewhere in Malaya to certain species of *Ficus* which have dangling or fastening roots. Rumphius described two forms, *alta* and *humilis*, of this fig-tree. Linnaeus did not specify which form he referred to, and perhaps included both in *F. benjamina*. The description of *alta* for the most part corroborates and supplements Rheede's of *Itty-Alu*. The plate, like many of Rumphius's, is very poor. Rumphius (p. 140) stated that his species might be *Itty-Alu*, but later (p. 142) cited *Itti-arealou* Rheede (*F. retusa* var. *nitida*) as a possible synonym. Most important in the identification of *alta* as var. *typica* is the habit: that of a strangling epiphyte with only a few surviving rootlets to make secondary trunks. *F. humilis*, although a lower tree, was said to have larger leaves and figs, and prop roots from the branches.

These forms have been variously allocated, but *alta* has been assigned to *F. benjamina* by Miquel (1867) 3: 288, Merrill (1917), and others. King and those who followed his synonymy included *Varinga parvifolia* without specifying the variety.

Loureiro's species.—The trees described by Loureiro (1790) 2: 665 as *F. indica* and *F. benjamina* should exchange names, according to Merrill (Je 1935) 24: 136-137.

When Loureiro described *F. indica* in Cochin-China he believed that he was referring to the ancient *F. indica*, now known as *F. bengalensis* L.; for he

cited Pliny and Clusius, who had discussed that tree, and he spoke of thick roots from the branches which fastened themselves in the soil, and of sub-lanceolate leaves. The vernacular name, *cây sanh*, as Merrill said, was one of those listed by Gagnepain (1929) 5: 766-767 for *F. benjamina* in Indo-China. However, Gagnepain (p. 778) cited *F. indica* Lour. as a reference for the modern *F. indica*, a species for which Miquel had resurrected the superseded and so non-valid name of the ancient *F. indica*. Although King, Merrill, and other eminent botanists have held valid Miquel's *F. indica*, that title should be supplanted by a new one.

Merrill also stated that Loureiro's description of *F. benjamina* applied about as well to Linnaeus's *F. benjamina* as to the modern *F. indica*. Although, as he said, the Cochin-China name *cây kùa* for *F. benjamina* Lour. was very like *cây dua* and *cây gia* which Gagnepain cited for *F. indica*, nevertheless Gagnepain listed *F. benjamina* Lour. under *F. benjamina* L. The striate leaves mentioned by Loureiro certainly belong to *F. benjamina*, but the many graceful rooting filaments from the reclining branches, and Loureiro's citation of *Varinga parvifolia humilis* and of Plukenet's polynomial suggest f. *haematocarpa* rather than var. *typica*.

F. picta.—Noronha said that this was a known species of Java. Miquel (1867) cited it as a synonym of *F. benjamina*, and King (p. 183) said that it probably was that species. Koorders & Valeton omit it.

F. pyrifolia.—Salisbury gave this name to a plant of *F. benjamina* in the garden at Chapel Allerton, England.

Wallich's specimens.—No. 4502 in Wallich's catalog is labeled *Ficus dictophylla* Wall. Sections A, B, and D, examined by King, have been allocated by him (p. 43) to *F. benjamina*. Section D already bore that name.

Blume's contributions.—Blume (1823) 35 reported *F. benjamina* from the Botanical Garden at Buitenzorg, and later (1825) gave a brief description. In (1836) 2: 16-21 he made a detailed summary of the knowledge concerning *F. benjamina*, which he believed was not *Itty-Alu*, was not native to Java, and seldom had secondary trunks. His description of the leaves suggests form *waringiana*, since it mentioned a long recurved acumen, a subrounded or slightly attenuated base, and basal veins. The receptacles were pea-like. Other characters were those of the var. *typica* of this study.

Blume compared *F. benjamina* with other species and rejected reports of it by Thunberg, Vahl, and Willdenow. He explained that Thunberg had misunderstood the composition of an old tree near Buitenzorg. Thunberg had thought that it was *F. benjamina*, and had sent a specimen of it under that name to van Royen, from whom it had come into Blume's possession. But the material sent proved to belong to *F. microcarpa* L.f., which had intertwined with *F. benjamina* to form the tree. *F. microcarpa* was considered independent by Blume, but was reduced to *F. retusa* var. *nitida* by later botanists.

Blume's statement as to the scantiness of secondary trunks should be discussed. Koorders & Valeton (1906) have said that *F. benjamina* always has a single trunk. This was the idea in the botanical gardens of Florida, also,

until recently. In 1949 I was told by several botanists or gardeners that some trees had the banyan habit, while others produced only short aerial roots from the branches. This observed variation in habit seems not to be due to a failure to distinguish varieties and forms, but to a real change in a given form, although not in an individual. For example: *"Ficus sp. Matthews* 2-184" seen at FTG had the leaves of *F. benjamina* var. *typica*, but possessed the banyan habit. It seemed to be the same as an unnamed *Ficus* at MK, which I was told could not be *F. benjamina* because of its habit. Neither tree had receptacles. Perhaps the second is *F. nuda* (see below). I have found the same to be true in form *waringiana*. This subject needs more investigation.

The haematocarpa series.—Two species to which Blume, probably in herbarium notes, gave the names *F. haematocarpa* and *F. neglecta* were described by Decaisne from Timor. Both descriptions read like one of *F. benjamina*, except for figs the size of *"Cerasus avium"* (whose diameter is about 2.5 cm. according to Rehder), and silky twigs in the case of *F. haematocarpa*. *F. neglecta* was said to be near *F. benjamina* and perhaps a variety of *F. haematocarpa*.

Blume (1836) 2: 18-19 compared *F. haematocarpa* with *F. benjamina*, but failed to find important differences except the size of the receptacles and the low banyan habit. He identified it with *Varinga parvifolia humilis*, thus extending its distribution to Amboina, and located it also in Semauw and the Moluccas.

Miquel (1847, *Urostigma haematocarpum*) and (1859) 1²: 346-347 spoke of stipules only 6 mm. long and of pea-size figs. He cited *Cuming* 1936, a Philippine specimen, said that it was called *Waringin* and added Java to the distribution. He, also, failed to find other significant differences from *F. benjamina*, and in 1867 allocated *haematocarpa* to *F. benjamina* as a variety. *F. neglecta*, also possessing small stipules, he eventually left as an independent species.

Both *F. haematocarpa* and *F. neglecta* and their various forms have been accepted as synonyms of *F. benjamina* by King, and by Koorders & Valeton (1906). They may carry with them the probably large-receptacled forms *F. striata*, *F. indica* Heyne ex Roth, and *F. pendula*, or these may belong to *F. benjamina* var. *comosa*. The possible synonyms *F. dicarpa* Blanco and *F. nepalensis* Blanco, suggested for *F. haematocarpa* by F.-Villar (1880) 200, have been eliminated by Merrill's statement (1918) 128 that both were *F. dicarpa*, which he could not reduce because of imperfect description. In (1923) 2: 69 he placed *F. dicarpa* under "Doubtful and Excluded Species". Perhaps Plukenet's polynomial and Loureiro's *F. benjamina* belong in this series.

The *haematocarpa* chain is distinguished from var. *comosa* by its red figs and, probably, by its banyan habit. It differs from the form *waringiana* by its larger figs and smaller stipules, and from var. *nuda* by the presence of basal bracts and a slightly larger fig. No Florida specimens were seen.

U. benjamineum.—Miquel's species is *F. benjamina* var. *typica*, as is evidenced by his citation (1867) 3: 267 of the Hooker specimen seen in

NYBG. An additional description of the species is found in Miquel (1859) 12: 346.

F. comosa Haines.—For this see the discussion of var. *comosa*.

F. waringiana.—In 1926 Dr. David Fairchild collected in Java for the United States Department of Agriculture receptacles of a Waringin fig-tree. Plants resulting from these were raised at Chapman Field and distributed as *P.I.* no. 67501. They were called *F. waringiana* after a name used by Dr. Fairchild, but because of a similarity of leaf and fig to *F. benjamina* they have now been allocated to that species. However there are certain characters which indicate a slightly different form, not worth publishing as a *forma*.

Dr. Fairchild (Exploring for Plants 438. 1930) spoke of the Javan tree as having small red figs and a banyan habit which developed a grove out of a single tree. Mr. Gaines R. Wilson of Coconut Grove in correspondence differentiated the tree from *F. benjamina* partly because of its "more erect growth, though still of weeping habit". A letter in 1948 from Dr. H. F. Loomis, Director of Chapman Field, said that no. 67501 has some buttress roots, a very few aerial roots, and few secondary trunks. My own observations confirm these varying reports for I have found trees with secondary trunks and others with merely dangling roots.

More significant criteria are found in the leaves of form *waringiana*, which are elliptic, usually twice or more than twice as long as wide, distinctly papillate on both surfaces, with an abrupt, rather long, slender and acute acumen, sometimes bent, a more or less cuneate base, and undifferentiated basal veins.

Additional examples seem to be: *P.I.* 124758, and 2-19 from FTG. *P.I.* no. 124232 has characters of both var. *typica* and form *waringiana*.

FICUS BENJAMINA var. COMOSA (Roxb.) Kurz, For. Fl. Brit. Burma 2: 446. 1877.

Ficus comosa Roxb. Pl. Coromandel 2: 14. pl. 125. 1798. *F. papyrifera* Griff. Not. Pl. Asiaticas 4: 394. Ic. pl. 554. 1854. (Possibly also *F. striata*, *F. nitida*, and *F. pendula*; listed in synonymy of var. *typica*.)

Var. *comosa* is described as differing from var. *typica* principally in its yellow figs 1.5-2.5 cm. ("cherry-size") in diameter. They are sessile, but narrowed at the base, and have 3 basal bracts about 4 mm. long. Roxburgh (1832) 3: 552-553 told of a deciduous hood over the rudiments of the young "fruit", and Koorders & Valeton (1906) 11: 119-120 have said that the young figs are enclosed by two triangular, sometimes hairy scales about 5 mm. long, and also that the basal bracts are larger than those of the typical variety. The leaves show basal veins and may be narrowed at their base. King has stated that the perianth parts are lanceolate-acuminate, and not spatulate. No secondary trunks have been reported, except by Williams (see below).

Type: From Circar Mts., eastern India.

Distribution: Eastern hills of peninsular India and base of the eastern Himalayas through Assam, Burma, and the Andaman Islands; probably also in the Malay Archipelago, southwest China, and the Philippines.

Specimens: Var. *comosa* has been rather doubtfully mentioned for Florida. No trees were seen by me. An herbarium specimen from India (AA) and one collected by L. H. and E. Z. Bailey at Port of Spain (BH) seem authentic, but the only one labeled *comosa* at NYBG appeared non-valid. However, some sheets showing rather large yellow figs, from Hainan and the Philippines, may prove to contain var. *comosa*. A greenhouse plant is reported from the Missouri Botanical Garden, St. Louis.

Additional illustrations: Johann Kerner,Hort. Semp. pl. 216. 1806 (not seen by me); Wight (1843) pl. 658; Koorders & Valeton (1916) pl. 735; L. H. Bailey ed. Stand. Cyc. Hort. pl. 1504. 1935. Pl. 3305 and the accompanying text by Lowe in Curtis's Bot. Mag. 61. 1834 seem inaccurate, although based upon specimens from the Circars. R. O. Williams, Guide Bot. Gard. Trinidad 13. pl. sect. 6. 1927 shows aerial roots forming trunks and calls var. *comosa* the Ceylon willow. This may possibly refer to *F. retusa* var. *nitida*, since I have found no report of *F. benjamina* in Ceylon, but notice that var. *nitida* is listed from there by Trimen (1885) 84.

Roxburgh (1798) contains certain contradictions which have been adjusted by other writers. For example, the colored plate shows peduncled figs, both yellow and purple of the same size, 2.5 x 2 cm.; although the text calls them sessile, with a contracted base, deep yellow when mature, and "gooseberry size". Green immature figs display basal bracts, which are missing from mature ones.

There has been some variety in the statements of authority for the name *comosa*. Roxburgh (1832) gives it as *F. comosa* Willd. Roxb., although Willdenow had cited Roxburgh as author and had used his description. Kurz has been acknowledged as the author of var. *comosa* by Haines (1924) 5: 828, but King is claimed by Koorders & Valeton (1906), probably because King did not refer to Kurz in this connection.

Both King and Haines thought that Linnaeus might have had *F. retusa* var. *nitida* in mind when he created the species *F. benjamina*, and therefore they advocated substituting the first valid name for an independent form. This they believed to be *comosa*. However Haines alone had the courage of his convictions. He said that in his area *F. comosa* was the tree seen.

F. papyrifera Griff. was accepted for *F. benjamina* by King and by Gagnepain (1929). It was described from Assam, and was said to have receptacles the size of a small apple. The plate corresponds to the leaf and fig of var. *comosa*.

The other suggested synonyms of this variety are linked together, and are separated from var. *typica* solely because of the cherry-size receptacle of *F. striata*, a species made by Roth from a specimen from the "East Indies," collected and named *F. nitida* by Heyne. *F. pendula* Hort. was listed by Sprengel (1826) 3: 781 as a synonym of *F. striata*, but Kunth (1846) 20 and (1847) III, 7: 250 declared that this was the species in the Berlin Royal Garden whose name, *F. pendula*, had already been published by Link. *F. pendula* has been accepted by most authorities as a synonym of the species *F. benjamina* L., but *F. striata* usually is included only tentatively. As was said above, these names may belong to the *haematocarpa* series.

Koorders & Valeton, although they quoted King's description, dissented somewhat from his views, saying that the leaves of var. *comosa* resembled

very little his plate and Roxburgh's, and that they could not distinguish certainly among *F. benjamina*, var. *comosa*, and *F. stricta* (Miq.) Miq.

FICUS NUDA OR FICUS BENJAMINA VAR. NUDA

Urostigma nudum Miq. Hook. Lond. Jour. Bot. 6: 584. 1847. *U. benjamineum* var. *nuda* (Miq.) Miq. Pl. Jungh. 1: 50. 1853. *Ficus nuda* (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 267, 288. 1867. *F. umbrina* Elmer, Leafl. Philip. Bot. 1: 49. 1906. *F. benjamina* var. *nuda* (Miq.)

Two distinquishing characters of this form are the pseudo-stalk, a narrow twisted continuation of the base of the ovid receptacle; and the absence of basal bracts in mature figs. The latter condition, from which the specific name is derived, is caused by the cutting off, at the base, of an enveloping involucre, as the receptacle grows.

In contrast to *F. benjamina* var. *typica* the following usually are present, although they may be slightly variable: banyan habit; rather narrower leaf-blades with a longer, slenderer, and more abrupt acumen, and a less rounded (rather wide-cuneate) base with one quite distinct pair of basal veins; and a receptacle which is corrugated when dry. There usually are two color phases of the receptacle, whitish, and red-brown; the latter larger than the other. The leaves of the two phases are alike.

In other respects, especially veining of the blade, var.*typica* and the *nuda* form are similar.

Type: *Cuming* 1932, from the Philippines.

First reports of distribution: Philippines (Miquel), Java (Miquel), Sumatra (Miquel), Burma (Kurz).

Specimens: (NY) Many from the Philippines, collected by Merrill, Elmer, and others, mostly checked by Merrill, originally labeled *F. benjamina*, *F. nuda*, and *F. umbrina*. Also fresh herbarium material from Chapman Field, H. F. Loomis coll. *U.S.P.I.* no. 80569. This came from the Philippines and, Dr. Loomis said, was listed first as *Ficus sp.*, then as *F. eugenioides* (under which name I collected it at FTG), and finally as *F. benjamina*. No. 80569 corresponds exactly to the above description of *nuda* and to authentic specimens at NYBG. It was growing also at MK.

History: King cited *F. nuda* as a synonym of *F. benjamina*, and Sturrock and Menninger (1946) 23 called "*F. eugenioides*" (probably the above) a subspecies of *F. benjamina*; but Merrill (1923) 2: 59 declared that it is a valid species. The type of *F. umbrina* Elmer was identified by Merrill as identical with the type of *U. nudum*, and that allocation was accepted by Elmer (1937) 9: 3457.

F. nuda var. *macrocarpa* Kurz (1877) 2: 446 was rejected by King as belonging to *nuda* and was re-named by him *F. kurzii* King, (1887-1888) 1: 47, 183; although King's plate of *F. kurzii* has been thought by others to resemble at least a variety of *F. benjamina*.

HOMONYMS OF F. BENJAMINA L. AND THEIR PROBABLE ALLOCATIONS

Allocated to *F. retusa* L.: *F. benjamina* of Graham, Guenther, Kunth, Link, Persoon, Roxburgh, Thunberg, Wight, Willdenow. Allocated to *F. rumphii* Blume: *F. benjamina*

of Houttuyn, in part. Allocated to *F. salzmanniana* (Miq.) ?: *F. benjaminea* Salz. ex Miquel. Allocated to *F. amplissima* J. E. Smith (*F. tsiela* Roxb.): *F. benjamina* of Wallich, Cat. no. 4503. Allocation doubtful: *F. benjamina* of Aiton (1813), Lamarck, J. E. Smith, Vahl, Vidal.

SUMMARY OF F. BENJAMINA L.

Representatives are found from northeastern peninsular India and border states through mainland and western Pacific islands to southwestern China. Var. *comosa* has in addition a restricted distribution in other parts of India. The species is widely cultivated for ornament.

F. benjamina differs from *F. retusa* L. in sometimes larger leaves, ovate or rather narrow elliptic, but never obovate, with a longer, slenderer and often bent acumen, and a sometimes cuneate, but never narrow base. The basal veins are shorter and sometimes missing or indistinct, and the lateral veins are more numerous and leave the midrib at a greater upper angle. They are paralleled by more veinlets than in *F. retusa*, so that the blade has a striate appearance.

The forms which have been accredited to *F. benjamina* may be separated as follows.

KEY

Figs sessile, although sometimes narrowed at the base, basal bracts present.
- Figs less than 15 mm. in diameter, red, yellow or purple.
  - Leaves ovate, sub-rounded at base, basal veins faint but usually visible, surfaces not or barely papillate ..... var. *typica*
  - Leaves elliptic, base broad-cuneate, basal veins indistinguishable, surfaces distinctly papillate ..... f. *warringiana*
- Figs 15-25 mm. in diameter.
  - Figs yellow or orange ..... var. *comosa*
  - Figs red; banyan habit ..... f. *haematocarpa*

Figs showing a pseudo-stalk, no basal bracts present at maturity ..... var. *nuda* (*F. nuda*)

Of these forms *haematocarpa* is the least known and may be allocated to var. *typica* on account of its figs' color, or to var. *comosa* because of the figs' size. More research on the habit of var. *typica* and the flowers of var. *nuda* is necessary. The last form may be an independent species.

FICUS ELASTICA Roxb. ex Hornem.

Ficus elastica as a source of rubber latex has been largely superseded by *Hevea brasiliensis* Muell. Nor is this "rubber plant" very frequently seen now in pots or tubs in northern climates, although at the height of its popularity 80,000 plants were said to have been sold in America in a single year, while in Germany it was so common that it was called the Berlin weed. In Florida, however, it has the distinction of being one of the largest species of *Ficus*. Its great height and spreading branches, of which the lowest are supported by prop roots, and its high sharp buttresses ending in straggling above-ground roots make it one of the state's plant spectacles.

Small (1933) 439 reported *F. elastica* as naturalized in pinelands and along roadsides in southern penisular Florida; and Nehrling's notes (1944) 1: 330 spoke of specimens as far north as Sanford, but indicated that its safe

cultivation was from Punta Gorda south. Mowry (1938) 51 and Royal Palm Nurseries (1938) 14 mentioned both the typical form of the species and its variety *variegata*. Sturrock & Menninger (1946) 23, 135 speak of *F. elastica* as susceptible to storm damage, but readily recoverable; and as a good tree for general use, although not for yards because of its widely spreading roots.

According to Miquel (1867) 3: 265 the leaves of *F. elastica*, which have furnished the principal characters used in the separation of varieties, are somewhat variable. In warm climates they may be large and "oblong," but in colder temperatures may show smaller, elliptical blades. There are smaller leaves on fruiting twigs than on purely vegetative ones. This leeway in size and shape seems to invalidate most of the reported varieties, including Miquel's. Therefore all except those apparently belonging to variety *variegata* are listed in the synonymy of the typical form of *F. elastica*.

Ficus elastica Roxb. ex Hornem. var **typica** M. F. Barrett, var. nov.

Ficus elastica Roxb. Hort. Beng. 65. 1814. *Nomen nudum*. *F. elastica* Roxb. ex Hornem. Hort. Bot. Hafn. Suppl. 7. 1819. *F. elastica* var. *bengalica* Blume, Bijdr. 446. 1825. *F. suborna* & *F. suborna* β Hb. Ham. ex Wall. Cat. no. 4557 D. 1831. As synonyms. *Nomina nuda*. *Visiania elastica* (Roxb. ex Hornem.) Gasp. Nov. Gen. Fic. 9. 1844. *Macrophtalma elastica* (Roxb. ex Hornem.) Gasp. Ric. Capr. 83. pl. 8. 1845. *F. taeda* Hort. ex Kunth, Ind. Sem. Hort. Berol. 1846: 14. 1846. As synonym. *F. cordata* Hort. ex Kunth, *Ibid*. As synonym. Not Thunberg or Ridley. *Urostigma elasticum* (Roxb. ex Hornem.) Miq. Hook. Lond. Jour. Bot. 6: 578. 1847. *U. elasticum* var. *latifolium* Miq. *Ibid*. *U. odoratum* Miq. Pl. Jungh. 1: 49. 1853. *U. circumscissum* Miq. Pl. Jungh. 1: 292. 1854. *U. karet* Miq. Fl. Ind. Bat. 1[2]: 348. 1859. *F. elastica* β *odorata* (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 265. 1867. *F. elastica* var. *minor* Miq. *Ibid*. 3: 287. 1867. *F. elastica* var. *karet* (Miq.) Miq. *Ibid*. *Stilpnophyllum elasticum* (Roxb. ex Hornem.) Drury, Handb. Ind. Fl. 3: 225. 1869. *F. duvivieri* Gentil, Liste Serres Chaudes 87. 1907. *Nomen nudum*. *F. elastica* var. *belgica* L. H. & E. Z Bailey, Hortus Sec. 308. 1941. *F. elastica* var. *rubra* L. H. & E. Z. Bailey, *Ibid*. *F. elastica* var. *rubinervis* Hort. ex Sata, Contr. Inst. Hort. & Econ. Bot. Taihoku Univ. 32: pt. I, 67. 1944.

Under native conditions a glabrous evergreen tree growing rapidly and becoming very large (to 60 m. high, crown diameter to 45-60 m.); sometimes starting as an epiphyte whose roots enclose the host's trunk, so that a new, apparently sculptured trunk is formed; aerial roots from the trunk of a large tree forming props and continuing over the ground, also forming high sharp buttresses near the trunk, and serpent-like roots extending to great distances; branching low, lowest branches horizontal or drooping, curved up at the apex; aerial roots from the low branches forming props and secondary trunks, very numerous (to 100 or more in largest trees); bark of trunk and branches gray and smooth at first; bark of roots reddish-brown, peeling in narrow strips or flakes; twigs straight, to about 1 cm. in diameter, green with pinkish lenticels; terminal bud covered with a single stipule which grows and persists until the leaves are half-grown or more; stipule pink or rosy, lanceolate, acute, sometimes becoming 20 cm. long; petioles about 5-10 cm. long, smooth; blades ovate, elliptical, or almost oblong, reported to reach 60 x 17.5 cm. in size (examples: 10 x 4, 17.5 x 6.5, 33 x 14 cm.); apex rounded, then rather abruptly apiculate or triangular acuminate; base equal, rounded or slightly cuneate; margin entire,

sometimes recurved or subundulate; texture thick, firm, leathery; upper surface smooth and glossy, dark green in typical form, marked with white or yellow lines or patches in var. *variegata;* under surface yellowish or glaucous green; midrib heavy, reddish at first; basal veins not much differentiated; lateral veins 30 or more, parallel to one another, leaving the midrib at about a right angle, united into a scalloped marginal vein, paralleled by reticular spaces elongated horizontally, and so appearing striate; receptacles axillary, paired, sessile, ovoid-ellipsoid, sometimes slightly angled, about 1.3 x 0.7 cm., greenish-yellow, sometimes dark-spotted, ostiole not prominent, apical bracts 3-5, young fig at first enveloped in an involucre made of connate basal bracts, involucre eventually circumscissile, leaving a scar or a cup with an entire or toothed margin around the receptacle; male, gall and female flowers in the same receptacle (according to King or Gagnepain); male flowers pedicelled, perianth of four ovate sepals, one stamen with an ovate, slightly nucronate, sessile anther; perianth of gall flowers with four sepals, ovary smooth, style sub-terminal, hooked; female flowers mostly sessile, four sepals, ovary smooth, style long, almost terminal, stigma large, sub-capitate.

Type: Garo Hills (Assam), India. *Matthew Richard Smith.*

Distribution: Northern India from the eastern Himalayas through Assam, Burma, and Malaya. Cultivated widely outdoors where the climate is suitable, and indoors as a pot or tub plant.

Common names: Rubber Plant, India or Indian Rubber Tree, Caout-chouc Tree, Snake Tree, Rubber Fig, Elastic Gum, Berlin Weed.

Economic importance: Formerly the principal source of rubber, which was obtained by processing the latex from the trunk, buttresses, and aerial roots.

Specimens: Trees seen at CF, Clearwater, Ed, FM, MK, MCC, Sar., and in many places in Miami. A particularly large tree, later broken off, was located near 2951 S. Bay Shore Drive, Coconut Grove. Herbarium specimens were examined at NYBG, BH.

Illustrations: Engler & Prantl *Natürlichen Pflanzenfamilien* 3 (1): pls. 49, 67. 1889. Garden & Forest (1889) 2: pl. 143. Haberlandt, *Botanische Tropenreise* ed. 2. 1910. King (1887-1888) 1: pls. 54, 83m. Koorders & Valeton (1916) pls. 740, 741. L'Horticulteur Universal 6: 108. 1845. Macmillan, Tropical gardening and planting ed. 4: 95, 96. 1935. Mowry (1938) pls. 39, 41. Walker, E. H. in Lingnan Sci. Jour. 6: 52. 1930.

Good descriptions: Gagnepain (1928) 5: 777-778. King (1887-1888) 1: 45-46. King (1888) 5: 508-509. Koorders & Valeton (1906) 11: 126-131. Miquel (1867) 3: 265-266. Roxburgh (1832) 3: 541-545, (1874) 3: 640-641.

AUTHORSHIP

In 1810 William Roxburgh, then the superintendent of the East India Company's gardens near Calcutta, received a present of a rattan basket shaped like a bottle and containing honey. Roxburgh, wondering why the honey did not leak through the rattan, emptied the basket and found it lined with an elastic sheet which he recognized as formed from the latex of some fig-tree. He communicated with the sender, learned that the gum came from a large tree near Sylhet in Assam, and arranged to have plants introduced into the Calcutta garden. In 1814 he listed *Ficus elastica* Roxb. in *Hortus Bengalensis*, but gave only a very brief description—not enough to constitute valid publication.

In a very few years *F. elastica* began to appear in other botanical gardens.

Breiter (1817) 153 reported it from Leipzig without naming an author, and Sweet (1818) 224 said that *F. elastica* Roxb. was introduced into the London Suburban Garden in 1815. Neither text described the plant. It is thought that the first valid publication was that by Hornemann of the Royal Botanical Garden at Copenhagen, in which the author was stated as Roxburgh.

Most writers have acknowledged Roxburgh as the originator of the specific name, although some have referred to his description in (1832). However, Link (1822) 2: 448 stated the authorship as "Roxb. Hornem.," and Kunth (1846) 14 and (1847) III, 7: 233 called it "Roxb. in Hornem." Since there is no proof that Roxburgh furnished Hornemann's description the correct form seems to be "Roxb. ex Hornem."

Another theory as to the author was expressed by Blume (1825) 446, who wrote "Nois." after the specific name. The reference probably was to Louis Claude Noisette, the author of *Le jardin fruitier* (1821), a treatise on fruit trees and vines. I have found no publication by him of *F. elastica*, but Steudel (1821) 340 listed this species, followed by "Nois. Breit. Zeyh." Breiter already has been mentioned. Johann Zeyher (1818) wrote about a garden at Schwetzingen in southwest Germany. Although I have not seen this text I believe that it, like those of Noisette and Breiter, did not provide authentic publication, since Steudel (1840) 636 cited Roxburgh as author. Noisette's name was combined with Roxburgh's by Colla, *Hortus ripulensis* 56. 1824, ("Nois. et Roxb."), and by Miquel (1859) and (1867) 3: 265 ("Nois." and "Nois. ap. Roxb."). The abbreviation "Nois." was thought by Brandis (1874) 417 and some others to be a contraction or misprint of *nobis*, and those writers therefore stated Blume as author. However, Brandis (1906) 603 substituted Roxburgh for Blume.

Other variations of this subject were "*F. elastica* L.," used by Duss (Ann. Inst. Col. Marseille) 3: 155. 1897; and the omission of the author, as by Griffith (1854) 4: 391. pl. 552. The important fact about all these is that their descriptions show that they referred to the same species.

ALLEGED SYNONYMS OF F. ELASTICA

F. suborna.—No. 4557 in Wallich's catalog is entitled *F. elastica* Roxb. Each of its four divisions represents the source of a set of specimens: *A* from Silhet (Sylhet), the location of the original *F. elastica*: *B* from the Botanic Garden at Calcutta, *C* from a place whose name is illegible, and *D*, *Ficus suborna* and *F. suborna* β from Hamilton's herbarium. The names in *D* are preceded by a question mark. Steudel (1840) 636 and Miquel (1847), (1859), and (1867) 3: 287 approved *F. suborna* Hb. Hamilt., for *elastica*, but Koorders & Valeton (1906) omitted it. King (1887-1888 and 1888) accepted all of no. 4557.

Gasparrini's species.—Gasparrini (1844) did not actually combine *Visiania* and *elastica*, although he referred to *elastica* as the basis of his new genus. However, that combination is accepted as a synonym by King (Ann.) and Koorders & Valeton (1906).

The following year Gasparrini published a plate showing flowers of *Macrophthalma elastica*. This name has been cited as a synonym of *U. elasticum* or *F. elastica* by Miquel, Drury (1869) 3: 225, King (Ann.), and Koorders & Valeton (1906).

Miquel's species.—Miquel made four species of *Urostigma*, all from Java. *U. elasticum*, a transfer of *F. elastica* Roxb., was again described and also illustrated in (1859) 1[2]: 347-348. pl. 23, and was referred to in some of his other writings. In (1867) 3: 265, 287 he returned it to *Ficus* and placed his three other species under it as varieties or synonyms of varieties.

Stilpnophyllum means "shining leaf." To this new genus Drury allocated *F. elastica* Roxb.

Horticultural names.—*F. taeda* and *F. cordata*, both from the Berlin Garden, were assigned to *F. elastica* by Kunth and cited again by Miquel (1867) 3: 287.

F. duvivieri, according to N. Taylor (1935) 1232, is like the typical form of *F. elastica*, except for thinner leaves.

ALLEGED VARIETIES

F. elastica var. *variegata* (*Gentil*) *Nehrling, Plant World in Florida* 174. 1933. [A. & E. Kay, ed.].—This is a horticultural variety with light green leaves bearing white or yellow lines or blotches. In Florida it was usually seen as a rather popular pot or tub plant which was sensitive to a dry atmosphere and had to be grown in partial shade because its lack of chlorophyll allowed the leaves to burn. However, Nehrling's notes have spoken of it as a tall dense tree without buttressed roots. Two such specimens are now (1949) growing in the patios of the Mira Mar Hotel at Sarasota.

Var. *variegata* was listed by Gentil, Liste Serres Chaudes 87. 1907, but was not described. Norman Taylor in L. H. Bailey, Stand. Cycl. Hort. 1232. 1935, stated that *F. elastica* var. *aurea* Hort. was a synonym of it. If all variegated forms are to be put under Gentil's name the synonymy probably would include *F. elastica albo variegata* in the 1937-1938 catalog of L. R. Russell Ltd. of England, p. 18; *F. elastica* var. *doeschera* L. H. & E. Z. Bail. Hort. Sec. 308. 1941; *F. elastica* var. *aurea-marginata Ibid.*, and others of nursery catalogs.

Varieties here included under the typical form of F. elastica.—Var. *bengalica* was named by Blume from a specimen which came to him from the Botanic Garden of Calcutta, and was said by him to have acuminate leaves with a subundulate margin. He had just described the leaves of *F. elastica* as acute and with a recurved margin. Miquel (1847) cited Blume's "forma *bengalensis*" (probably a misquotation of *bengalica*) under *U. elasticum*. Brandis (1874) 418 mentioned Blume's variety without description. From its origin and distinguishing characters it seems to belong to the typical form.

Miquel's *Urostigma elasticum* var. *latifolium*, he thought, might be a

species. However, it was omitted from his later texts. It was based upon an herbarium specimen from Assam which had leaves 25 x 14 cm. in size. These are almost the same proportions as those of a smaller leaf of *F. elastica* figured by Wight (1843).

The species of *Urostigma* made by Miquel and allocated by him to some form of *F. elastica* bear a more confused relationship to one another than appears in the synonymy. The first to be published, *U. odoratum*, was described again in Miquel (1859) 1²: 348 and was illustrated in pl. 24 B of that book. It was characterized principally by a cuneate blade base and by blades 9-16.5 x 5-8 cm. A specimen by this name in the herbarium of the New York Botanical Garden from the Leiden-Batavian herbarium has leaves to 18 x 10 cm. and agrees well with the typical form of *F. elastica*. Miquel (1867) 3: 265 called this species of *Urostigma*, *F. elastica β odorata;* but on p. 287 listed it as the first synonym under *F. elastica* var. *karet*. King (1887-1888) and Koorders & Valeton (1906) cited it as a synonym of *F. elastica* var. *minor*.

U. circumscissum received its name from the mark left when the bracts of the young receptacle dropped off as if cut away. It had leaves 5-7.5 cm. long and was known in Java as *Karet*. Miquel (1867) 3: 287 gave it as example (probably type) of *F. elastica* var. *minor*, and King and Koorders & Valeton approved this reduction.

U. karet was said by Miquel to have leaves like *U. elasticum* (a third species to bear the vernacular name of *Karet*) except for a greater width and distincter, more distant veins. Miquel (1867) 3: 287 cited it as the second synonym of *F. elastica* var. *karet*. King (1887-1888) transferred it to var. *minor*, and Koorders & Valeton did not dissent.

By including rather large-leaved forms in Miquel's variety *minor* King destroyed the significance of the specific name. Nevertheless, before revalidating varieties *karet* and *minor* it is well to consider their author's remark, already quoted, about variable leaves.

Varieties *belgica* and *rubra*, proposed by Bailey and Bailey, seem to resemble the typical form of the species. *Belgica* was said to have red juvenile leaves, a not uncommon color in *Ficus*, and *rubra*, the authors thought, might be a synonym of *belgica*. Var. *rubinervis* Hort. ex Sata, which was said to have a red midrib on the lower surface of the blade, may belong with *belgica* and *rubra*.

SUMMARY

Best-known in this country of all the fig-trees with the exception of *Ficus carica* L., the fig of commerce, *F. elastica* is one of the largest in Florida.

As a result of its earlier popularity as a house plant several varieties have been produced, of which the mottled leaved var. *variegata* is the most conspicuous.

Ficus elastica as a source of material for rubber has been superseded by *Hevea brasiliensis*.

FICUS FULVA AND FICUS HIRTA

Ficus fulva Reinw. ex Blume and *F. hirta* Vahl, two species found especially in Indonesia and China, have type-varieties which resemble each other in their possession of both unlobed and palmately 3- or 5-lobed leaves, and in a general roughness and hairiness of the external surfaces. Both species belong to subdivision *Eusyce* of *Ficus*, which is characterized in part by receptacles of two sorts: one, usually ovoid, containing male flowers with two stamens, and gall flowers; and the other, which is globose, holding female flowers.

The reason for including *F. fulva* and *F. hirta* in one study lies not only in their similarity, but also in their alleged varieties, which may have been incorrectly allocated by some authors and so might affect the synonymy of the two species.

Ficus fulva var. typica (King) M. F. Barrett, comb. nov.

F. fulva Reinw. Hb. ex Blume, Cat. Gew. Buitenzorg 36. 1823. *Nomen nudum. F. fulva* Reinw. Hb. ex Blume, Bijdr. 478. 1825. Not Sprengel, Hort. ex Kunth, Miquel ex Glaziou, or Elmer. *F. reinwardti* Link & Otto, Icones plantarum rariorum 1: 61. pl. 31. 1828-1831. *F. fulva* var. *pubescens* Zoll. Hb. ex Miq. in Zoll. Syst. Verz. 92. 1854. As synonym. *F. apiculata* Miq. *Ibid.* 98. 1854. Not Miq. 1848. *F. chloroleuca* Miq. Fl. Ind. Bat. 1[2]: 294. 1859. *F. suborbicularis* Miq. Fl. Ind. Bat. Suppl. 1: 425. 1860. *F. fulva* γ *orbicularis* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 269. 1867. *F. fulva* forma *typica* King, Ann. Bot. Gard. Calcutta 1: 149. pl. 187. 1888. *F. dumosa* King, *Ibid.* 1: 151. pl. 190. 1888. *F. hirta* Treub, Annales du Jardin Botanique de Buitenzorg II, 3: 124. f. 16-25. 1902. Not Vahl or Roxb. (To this synonymy that of *F. hirta* var. *roxburghii* perhaps should be added.)

A shrub, or a tree reported to 15 m. high; tree-trunk single, diameter reported to about 25 cm., straight, slender, divided into branches about halfway up; branches few, spreading horizontally, drooping; young bark bearing conspicuous lenticels and stipular scars, older bark smooth to cracked, but not usually furrowed; twigs few, about 1-1.5 cm. in diameter, at first bearing long tawny hairs, becoming almost bare, green to reddish-brown or gray, rough; terminal buds 1-3 cm. long, ovate, each covered with an acuminate greenish or purplish hairy stipule which may elongate to 6 cm.; petioles 2.5-14.5 cm. long, stout, hairy at first; blades membranous or thin-leathery; roundish, in young plants often 3- or 5-lobed, lobes ovate, the middle one much the largest, side lobes narrower, extending less than halfway in towards the midrib, their upper edge almost perpendicular to the line of the midrib, sometimes two basal lobes or suggestions of such, whole blade 10-35 cm. in diameter (examples: 16 x 12.5, 24 x 18, 28 x 23 cm.); blades in older plants less often lobed, but roundish, rhombic-ovate, or broad-ovate, examples of size: 23 x 15, 29 x 19 cm.; apices of all blades acute or with a short acumen to about 1 cm. long; base broad, cordate or rounded; margin denticulate or shallow-dentate, but sometimes entire or sinuate, teeth sometimes ciliate; upper surface medium green, becoming dark green in dried specimens, dull, rough with whitish papillae, each bearing a hair, becoming less hairy; under surface tan-colored in dried specimens, velvety on the reticulum, sometimes with long soft hairs on the large veins, color of hair tawny or yellow, becoming lighter or gray; midrib very heavy, continuous to apex, hairy; 1-3 sets of basal veins, the

number somewhat dependent upon the number of lobes, but usually less than at first glance because of the branches of the largest pair, this pair extending more than halfway up the blade; 4-7 sets of lateral veins in the largest lobe, forking and uniting near margin in shallow indentations; transverse veins connecting the laterals at almost a right angle; reticulum and checkered background present; receptacles (figs) axillary, often crowded, typically paired, sessile or very short-peduncled; ovoid to about 2.5 x 1.5 cm., globose or depressed-globose 1.5-4 cm. in greatest diameter; apex sometimes becoming raised by three hairy red apical bracts; basal bracts 3, ovate and apiculate, reddish and light-hairy; surface of figs yellow- or rusty-hairy at first, color green to red or orange; male flowers near the apex of the ovoid receptacle, sessile, sepals three, broad-oblong or ovate, stamens two, filaments short, anthers oblong; gall flowers in receptacle with male flowers, sessile or short-pedicelled, sepals 5, narrow lanceolate, ovary smooth, ovoid, style short, lateral, stigma infundibuliform; female flowers in globose receptacles, like the gall flowers except for a longer, filiform style, a columnar stigma, and a minutely tuberculate ovary.

Type: Reinwardt. Java. Mountains along margins of rivers.

Distribution: Sumatra, Java, Celebes, Philippines, Indo-China, Hainan, S.W. China. ?India (if *F. hirta* var. *roxburghii* is transferred to *F. fulva.*) This species is not common in Florida, although its small size might make it useful for certain locations.

Economic importance: Leaves as fodder for horses.

Good references additional to those in the synonymy: De Vriese (1847) fasc. 1 (including illustration). Gagnepain (1928) 5: 804-805. King (1888) 5: 531. Koorders & Valeton (1918) pl. 774 (lobed leaf), (1906) 11: 252-256.

Specimens: A growing plant of var. *typica* was examined at CF in 1937, and in 1949. In 12 years the shrubby tree had grown little in height. Its height was 2.1 m. and its crown diameter 6 m. Herbarium specimens (NYBG) from Indo-China, Hainan, and China are more numerous than those from the Malay Archipelago and have more abundant, longer, and yellower hairs. Some, collected in Hainan, are labeled "*F. fulva* Dunn & Tutcher (an Reinw.?)," but seem like others about which apparently there is no question.

Examples: Otto Kuntze 4887, Java, labeled "v. contracta." *Poilane* 10822, Indo-China. *C. Wang* 35428, Hainan. *S. K. Lau* 1935, Hainan. *C. L. Tso* 21661, Kwangtung Prov., China. *Edano* 77382, Palawan, Philippines, labeled *F. chrysocarpa* Reinw.

SYNONYMS OF F. FULVA VAR. TYPICA

F. fulva.—Blume's list of wild and cultivated plants in the Botanical Garden at Buitenzorg gave no description of *F. fulva.* According to De Vriese *F. fulva* was so named by Reinwardt in his journal. Blume (1825) said that the species was near *F. hirta* Vahl, and that the native name was *Amberong mirrha.*

F. reinwardti (*i*).—This specific name, without the final *i*, was given to a greenhouse plant which had been brought from Java. De Vriese and others have stated that it is a synonym of *F. fulva.*

Synonyms from Miquel.—Some confusion has been caused by Miquel's creation of species now recognized as synonyms of *F. fulva,* and by his occasional duplication of names.

Sprengel (1826) 3: 779 had called a Brazilian plant, *F. fulva*. This was allocated by Miquel in 1847 to the genus *Urostigma*. When, later, Miquel transferred his *Urostigma* species to *Ficus* he must have faced a problem, since he was familiar with *F. fulva* Reinw. ex Blume and knew that it was not Sprengel's plant. Apparently he tried to resolve the dilemma by asking (1867) 3: 297 whether the Brazilian tree was *F. holosericea* Schott ap. Spreng. *F. fulva* Miquel was listed from Brazil by Glaziou (in Bull. Soc. Bot. France 59: Mém. 3^{s}: 641. 1913), who referred to Miquel's description of *U. holosericeum* in Mart. Fl. Bras. 4^{1}: 92. 1853. But Miquel did not mention *F. fulva* in that reference.

A glabrous, unlobed, and small-leaved specimen, *Wight* 1916, was named *U. apiculatum* by Miquel (1847) 6: 570. In 1854 he gave the title *F. apiculata* to specimen 651 in Zollinger's herbarium, which there had been called *F. fulva* var. *pubescens*. In (1867) 3: 269 Miquel quoted Zollinger's description of var. *pubescens*, and on p. 290 listed *F. apiculata* (1854) with the synonym *F. chloroleuca* Miq. However, on p. 286 he had listed also another *F. apiculata*, referring to his *U. apiculatum* (1847). From the descriptions it is obvious that *U. apiculatum* is distinct from *F. fulva*, but that *F. apiculata* (1854) and *F. chloroleuca*, both from Java, belong to Blume's species.

A second *F. fulva* from Zollinger's collection, no. 811, from Java, because of its lobed and unlobed leaves also seems to be var. *typica*, although Miquel allocated it to *F. chrysocarpa* Reinw. ex Blume.

A Sumatran species was described by Miquel as *F. suborbicularis*. In (1867) 3: 290 he stated this as the type of *F. fulva* γ *orbicularis*, which he described on p. 269 from Celebes and "Batjan."

King's contributions.—King separated var. *minor* from "*F. fulva* forma *typica*" and cited two synonyms for the variety. By elimination of these from the synonymy of the species as a whole the remaining names are assumed to have been allocated by him to the typical form. These are *F. reinhardtii*, *F. apiculata* Miq. 1854, and *F. suborbicularis*. Of the last named King remarked that it "scarcely deserved separation even as a variety."

Additional synonyms from Koorders & Valeton.—These authors said (1906) that King had determined most of the specimens in Koorders' herbarium, and that there were two forms of the species in Java, corresponding to King's forma *typica* and var. *minor*. They added *F. chloroleuca* Miq. and *F. hirta* Treub to King's synonymy of the species as a whole.

F. hirta Treub.—Treub published a study of the female organ and embryogeny of the species which he believed was *F. hirta* Vahl.

F. dumosa King.—An herbarium sheet at the Bailey Hortorium, Ithaca, N. Y., cites this name as a synonym of *F. fulva*. King's description of *F. dumosa* was based on specimen *H. O. Forbes* 229 from E. Sumatra, and was located in King's text between *F. hirta* and *F. chrysocarpa* Reinw. ex Blume, which probably is *F. aurata* (Miq.) Miq. The only character of *F. dumosa* as stated by King which has not been reported also for *F. fulva* is the number of sepals (4) in the male flowers. The gall and female flowers were said

to have 5 sepals. The male sepals were of the same shape as those of *F. fulva*. Their number did not vary more than is sometimes the case in related species. The plate pictured a 5-lobed leaf like that shown for *F. reinwardti* by Link & Otto. It had rather more deeply cut and slanting lobes than usually are found in *F. fulva*.

Forbes (1925) 63: suppl., 111 listed this species from Java, also, and gave its native name as *Hamberang-minjak*. This is the same as one of the vernacular names cited for *F. fulva* by Koorders & Valeton, and has almost the same sound as that mentioned by Blume.

FICUS HIRTA Vahl

The specific name *hirta* refers to the hairy surfaces of twigs, leaves, and figs, which are more bristly than those of *F. fulva*.

Specimens labeled *F. hirta* Vahl in the New York Botanical Garden's herbarium show a range of blade-shapes which may be roughly classified as (1) unlobed, narrow and willow-like; (2) unlobed, broad lanceolate or oblanceolate; (3) unlobed or lobed, ovate, elliptic or obovate; (4) deeply indented with very narrow lobes, sometimes also unlobed and willow-like. Of these groups the third agrees best with Vahl's description, and, as King has said, is the typical form. Here it is designated as var. *typica*.

Ficus hirta Vahl var. **typica** M. F. Barrett, var. nov.

F. heterophylla Lam. Enc. Méth. 2: 499. 1788. Not L.f. or Blanco. *F. hirta* Vahl, Enum. 2: 201. 1806. Not Roxb., Sieb., Treub, F. Villar, on some writers on India. *F. setosa* Blume, Bijdr. 477. 1825. *F. setifera* Steud. Nom. Bot. ed. 2: 638. 1840. *F. hirta* var. *integrifolia* Miq. Fl. Ind. Bat. 1[2]: pl. 18 A. 1859. *F. hirta* var. *setosa* (Blume) Miq. *Ibid.* pl. 18 B. 1859. *F. porteri* Lév. & Van. in Fedde, Rep. Spec. Nov. 8: 550. 1910. *F. hirta* var. *imberbis* Gagn. in Lecomte, Fl. Gén. Indo-Chine 5: 804. 1928.

Usually a small shrub 1-3 m. high (reported to 6 m.); surface of twigs, leaves, and receptacles hairy-bristly, yellowish, reddish, or tawny to gray, sometimes becoming almost bare; twigs to 7 mm. in diameter, tan-colored, striate; stipules ovate-lanceolate, 1.3-3 cm. long, acuminate, strigose or hispid to puberulous, deciduous; leaves symmetrical, unlobed and lobed on same or different branches or trees; petioles to 8 cm. long, very hairy; unlobed blades elliptic, ovate, obovate, broad-lanceolate or oblong, 10-26 x 4-15 cm. (examples 12 x 8, 16 x 8, 17 x 6, 25 x 10 cm.); lobed blades found especially on young trees, lobes mostly 3, in upper half of blade, size of blade (examples) 14 x 8, 18.5 x 9.5 cm.; middle lobe ovate (examples: 7 x 3.5, 9 x 4 cm.), side lobes narrower, only slightly flaring, upper edge at an acute angle to the line of the midrib (examples: 3 x 2, 4 x 2 cm.); apex of blade or of lobes acuminate, sometimes narrowed; base often wide with almost parallel vertical margins, rounded, subcordate, or truncate, or narrowed a little and obtuse; margin usually serrate, sometimes with ciliate teeth (example: 4-5 teeth to 1 cm.), sometimes sinuate; texture membranous, thin; upper surface with bristle-bearing papillae, becoming bare, rough; under surface bristly, tomentose, or pubescent, glabrescent but retaining hair longest on veins; basal veins one pair, but appearing more because of branches, extending more than halfway

up the blade; lateral veins 4-7-10 sets, upper angle at midrib 50°-60°, forking near the margin and uniting with other laterals in a marginal vein; transverse veins almost straight and right-angled, uniting laterals; reticulum well-marked except when obscured by hairs; checkered background present; receptacles axillary, near the apex of the twigs, typically paired, sessile or with a peduncle to 5 mm. long; male and gall flowers in ovoid figs; female in globose receptacles; figs 6 mm. to 15 or rarely to 25 mm., tawny or yellow-hairy, bristly, surface greenish yellow or brownish; sometimes several apical bracts prolonging apex; basal bracts 3, ovate, about 2 mm. long, acute, pubescent; flowers said to be sessile in male, pedicelled in female; sepals 4, narrow; stamens 2; stigma of gall flowers said to be infundibuliform in gall flowers, cylindric in female; achene minutely tuberculate.

Type: China, Java.

Distribution: Blume (1825) stated that Javan specimens came originally from China. Collected also in Burma, Sumatra, Indo-China, Hainan, and S.W. China.

Economic importance: Very young top shoots eaten raw, also reecptacles, which are sweet. (Ochse).

Some references additional to those in the synonymy: King (1887-1888) 1: 149-151, pl. 188. Koorders & Valeton (1906) 11: 250-252, (1918) pl. 775. Kurz (1877) 2: 449-450. Ochse *Vegetables of the Dutch East Indies* 500-501. f. 310. 1931. Solms-Laubach in Bot. Zeitung 43: pl. 5, f. 22-27. 1885.

Examples of specimens: Hallier (no nos.) Oct. 29, 1894 and Nov. 26, 1894, from Java, determined by Valeton. *C. Wright*, Hongkong. *N. K. Chun* 40333 and many others from Kwangtung Province, China. *Y. Tsiang* 6347, Kweichow Province, China. *C. Wang* 34362, Hainan. A shrub at CF was examined in 1937. The species was not seen elsewhere, or reported, so far as I know, in Florida.

ALLEGED SYNONYMS OF F. HIRTA Vahl

"*F. heterophyll'a* Hb. Lam." was proposed as a synonym by Gagnepain (1928) 5: 803. Lamarck believed that he was describing an herbarium specimen of *F. heterophylla* L.f., although he said that the Linnean species differed from his own plant in its glabrous figs. Lamarck's description is an excellent one of *F. hirta* Vahl, and is very different from *F. heterophylla.* It was excluded from the references for *F. heterophylla* by Poiret (1811-1812) 2: 648, who said of that species: "Non Lam. Dict.," and it was omitted by King and others.

F. hirta.—Vahl's brief description was based upon a specimen from China with trifid leaves and hispid figs the size of a pea; and upon another, from Java, with both unlobed and lobed leaves and hispid figs twice as large as those of the Chinese specimen. Koorders & Valeton (1906) have remarked that the species is not widespread in Java. This was borne out by the paucity of Javan specimens and the large number from China in the herbarium of the New York Botanical Garden.

Not all reports of *F. hirta* apply to var. *typica.* Sometimes they represent the whole species, and occasionally they appear to refer to a different variety or even to a different species. *F. hirta* F.-Villar has been judged doubtful or to be excluded from Philippine species by Merrill (1923) 2: 69, *F. hirta* Treub was allocated to *F. fulva* by Koorders & Valeton, and *F. hirta*

Sieb. ex Sieb. & Zucc. was declared a synonym of *F. carica* by Miquel (1866) 2: 199. *F. hirta* as recorded by Brandis (1906) 608 and by Cowan & Cowan (1929) 125 is the so-called var. *roxburghii*. To this variety belong also *F. hirta* Roxb. (1814) 65 and (1832) 3: 531, Wight (1843) pl. 672, and Drury (1869) 3: 235.

Gagnepain described *F. hirta* Vahl without mention of lobed leaves, which he put under var. *roxburghii*. The unlobed leaves of the species present a problem when they appear without the lobed ones, since they are similar to those of such small-receptacled forms as *F. fulva* var. *minor* and *F. aurata* (see later pages).

The setosa group.—Blume's description of *F. setosa* from Java is a much better one of *F. hirta* than his of that species.

The name *F. setosa*, without an author, was used by Hooker & Arnott, (Botany of Capt. Beechey's voyage 216. pl. 49. 1836) for specimens collected in China. This reference has not always been accepted for *F. hirta*. The description and plate look rather like *F. aurata*. Steudel chose the specimens of Hooker & Arnott to bear the name *setosa*, and therefore allocated Blume's species, as a synonym, to a new name, *F. setifera*. However, after *F. setosa* Blume he asked "non? Hook. & Arn.)".

Miquel, who previously had accepted *F. setosa* Blume with *F. setifera* as a synonym, and had allocated *F. setosa* Hook. & Arn. to *F. hirta* Vahl as a synonym, in (1859) 12: 297 collected the first three of these names under *F. hirta*. Although his text mentioned no varieties the accompanying plate showed an unlobed leaf labeled var. *integrifolia* and also two lobed blades, one with three lobes like var. *typica* and the other with two, one being a side lobe. The lobed leaves were designated var. *setosa*. In (1867) 3: 290 Miquel omitted from *F. hirta* both varieties and *F. setosa* Hook. & Arn.; but King and Koorders & Valeton accept both *F. setosa's* and also *F. setifera*.

F. porteri Lév. & Van., which has broad-lanceolate blades, has been identified as *F. hirta* Vahl by Rehder (1929) 10: 126 and (1936) 17: 77, and by Handel-Mazzetti (1929) 7: 100. Rehder examined in Edinburgh type specimen *J. Cavalerie* 3594 from Kweichow Province, China. *F. laus-esquirol i* Lév., *Esquirol* 3634, also is *F. hirta*, but other specimens and the original description belong to *F. hirta* var. *roxburghii*, according to Rehder.

Necalistis aspera Raf. Sylv. Tell. 58. 1838.—An early issue of *Index Kewensis* claimed that this was a synonym of *F. hirta*. But Rafinesque, who usually omitted the original authors when transferring their species from *Ficus* to his new genera, listed *F. aspera* as the type of *N. aspera*. If the reference is to *F. aspera* Forst. f., a valid species, it bars *N. aspera* from *F. hirta*.

ALLEGED VARIETIES OE F. HIRTA AND F. FULVA

Although these varieties may not be present now in Florida they should be discussed because of their debatable positions in synonymy and on the chance that at least the newest ones may be introduced into that state.

The first two following, spoken of by Chun (below) as forms or varieties of *F. hirta*, have rather willow-like leaves and/or 3-, 5-, or 7-lobed blades deeply pinnatifid like those of some Japanese maples.

FICUS HIRTA VAR. HIBISCIFOLIA (Champ. ex Benth.) Chun, Sunyatsenia 1: 225. 1924.

F. hibiscifolia Champ. ex Bentham, Hook. Jour. Bot. & Misc. 6: 77. 1854.

This form, from Hongkong, later was declared by Bentham a synonym of *F. hirta* Vahl. An example cited by Chun, *C. L. Tso* 20475, Kwantung Province, China, is a shrub. A typical leaf of this number, seen at NYBG, measures 17.5 cm. long, has a middle lobe 14.5 x 2.5 cm., side lobes about 8.5 x 2 cm., and an entire to faintly toothed ciliate margin. The dry figs measure 1. cm. in diameter. Other herbarium specimens labeled var. *hibiscifolia* have deeper teeth. *C. Wang* 32939 from Hainan, like some other specimens, has no lobed leaves. Its blades are entire, ciliate, and measure up to 12 x 2.5 cm. The figs are 1 cm. in diameter. This variety is very hairy or bristly, at least at first.

FICUS HIRTA VAR. PALMATILOBA (Merr.) Chun, Sunyatsenia 1: 225. 1934.

F. palmatiloba Merr. Philip. Jour. Sci. 21: 340. 1922. *McClure* 8066.

Merrill (Je 1935) 24: 138 placed this under *F. simplicissima* Lour. (1790) 2: 667 as a synonym, referring to Gagnepain (1928) 5: 791, who there and on p. 748 had suggested that synonymy as possible.

Chun distinguished var. *palmatiloba* from var. *hibiscifolia* by its more deeply cut lobes, which are lanceolate, entire, and abruptly caudate. He listed an example of his variety as *N. K. Chun & C. L. Tso* 43449 from Hainan. An herbarium specimen of this number at NYBG agrees well with Merrill's original description, but had been cited by Chun as an example of *F. hibiscifolia*, also. It is a small shrub with yellow-red figs about 5 mm. in diameter. Merrill had listed the receptacles as measuring 1 cm.. The two bottom lobes of the blade are very short and flaring and the other lobes measure about 7.5-9.5 x 1 cm. each. The margin is entire. All surfaces are rough and only slightly hairy. This herbarium sheet, although labeled var. *palmatiloba*, also bears the penciled title *F. laceratifolia* Lév. & Van. which, according to Rehder (1929) 10: 130, is a very distinct species because of its strongly dentate or lobulate and caudate leaves.

Of the other herbarium specimens labeled var. *palmatiloba*, *Y. Tsiang* 2215 has one entire and one toothed leaf and figs 1.3 cm. in diameter. Apparently it is the same as var. *hibiscifolia*, *C. L. Tso* 20475. *H. Y. Liang* 64330 (*F. hirta*) has both willow-like and lobed blades. *Y. Tsiang* 6372, which seems to be this variety, although not so labeled, has 5-lobed toothed leaves 35 x 24 cm. in size. Another large-leaved specimen, *A. Henry* 11599 A, labeled *F. hirta*, seems to shade into var. *typica*. All are Chinese.

From the specimens seen, varieties *hibiscifolia* and *palmatiloba* are much alike. It is possible that both are synonyms of *F. simplicissima*. They certainly have very few characters of *F. hirta*.

FICUS HIRTA VAR. IMBERBIS Gagnep. in LeComte, Fl. Gen. Ind.-Chine 5: 804. 1928.

Gagnepain said that the leaves of this variety were like those of var. *roxburghii*, but that only short scanty hairs were present. As his conception of var. *roxburghii* seems to differ from the early descriptions it is possible that he found a more or less glabrous specimen of var. *typica*.

FICUS HIRTA VAR. ROXBURGHII (Miq.) King, Ann. Bot. Gard. Calcutta 1: 150. pl. 189. 1888.

Ficus hirsuta Roxb. Hort. Beng. 65. 1814. *Nomen nudum*. Not Velloso or Miquel. *F. hirta* Roxb. *Ibid*. *Nomen nudum*. Not Vahl. *F. triloba* Hb. Hamilt. ex Wall. Cat. no. 4491. 1831. *Nomen nudum*. *F. hispida* Roxb. MSS. ex Wall. *Ibid*. As synonym. Not L.f. or Blanco. *F. hirsuta* Roxb. Fl. Ind. 3: 528. 1832. *F. hirta* Roxb. *Ibid*. 3: 531. *F. triloba* Buch. ex Voigt, Hort. Sub. Calcuttensis 284. 1845. *F. roxburghii* Miq. Hook. Lond. Jour. Bot. 7: 456. 1848. Not Wallich. *F. esquiroliana* Lév. Bull. Geog. Bot. 24: 252. 1914. *F. laus-esquirolii* Lév. Fl. Kouy-Tchéou 425, 431. 1915. *F. neo-esquirolii* Lév. *Ibid*. As synonym. *F. hirta* var. *roxburghiana* Cowan & Cowan, Trees N. Bengal 125. 1929.

King described this variety as densely rufescent, with leaves deeply lobed or not, ovate or ovate-round, 15-30 cm. long; and receptacles 1.3-2.5 cm. in size. Pl. 189 shows a (reduced) blade with the acute-angled lobes and the bulbous base of *F. hirta* var. *typica*, a full-sized globose female receptacle about 1.6 cm. in diameter, and an ovoid male fig almost 3 x 2 cm. The flowers have four sepals and are almost the same as those shown by him for the typical form. In short, King's variety seems to be a larger-leaved, bigger-receptacled form of *F. hirta* var. *typica*. He said that Vahl's form of *F. hirta* was almost entirely supplanted in northern India by this variety, of which he had never seen a specimen from farther south. The two varieties, he declared, met in the Khasia Hills (in the western part of Assam).

Type: M. R. Smith, Sylhet, Assam.
Distribution: Northern India, Sikkim, Assam. ?Burma, ?SW China. Not in Florida.
References and specimens: See following text.

SYNONYMY AND SPECIMENS

This variety is long in synonymy, but short and questionable in the specimens which must be considered with the synonyms.

King included in the synonymy of the whole species *F. hirta* Vahl all the different forms to his date which are cited in the synonymy (above) of this variety, except *F. hirta* Roxb. However he singled out *F. roxburghii* Miq. and *F. triloba* Hamilt. as possible bases for the name of this form. At first King preferred the former name, since some leaves were not three-lobed; but in (1888) 5: 531-532 he used the combination "*F. triloba* Ham. (*F. roxburghii*)" as a synonym. Miquel had done the same thing. Although in 1848 he had included *F. triloba*, with the three names ascribed to Roxburgh, under *F. roxburghii*, in (1867) 3: 270 and 290 he substituted *F. triloba* as the name of the species, since Wallich (1831) had designated another plant as *F. roxburghii*.

King's conception of var. *roxburghii* was not entirely original, since Bentham (1861) 329 had said that *F. hirta* Vahl of S. China and the Malay Peninsula was replaced in "Assam and Silhet" by the broad-leaved "(species or variety?)" *F. roxburghii* Miq. However, King's text shows evidence of field observations, examination of different sets of the specimens listed in Wallich's catalog, and a study of the literature which he lists.

F. hirta Roxb. and *F. hirsuta* Roxb.—The specimens to which Roxburgh gave these names had unlobed, and 3- or 5-lobed leaves respectively and had been sent to him from Sylhet in 1810. They were described in detail in Roxburgh (1832), but by that time Vahl's *F. hirta* was well known, and the specific title *hirsuta* had been preempted by Velloso. Roxburgh's species were well illustrated by Wight (1843) pls. 670 (*F. hirsuta*) and 672 (*F. hirta*).

It must be remarked, however, that the leaves in these plates look much more like *F. fulva* than like *F. hirta*. The ovoid figs measure about 4 cm. in greatest diameter, larger than those of King, and the flowers have 3 or 5 sepals instead of the four mentioned by King. Miquel in Ann. Sci. Nat. III, 1: 32. 1844 gives the same number of sepals.

F. triloba and *F. hispida* Roxb.—In Wallich's catalog *F. triloba*, probably named by Buchanan-Hamilton, had two divisions, each occupied by a place-name. After these Wallich remarked: "Est *F. hirta* et *F. hispida* Roxb. MSS." Since there is no mention of *F. hispida* in Roxburgh (1814 and 1832) it is likely that Wallich substituted that name by mistake for *F. hirsuta*. *F. hispida* L f. had been published in 1781. Wallich's *F. triloba* was published by Voigt.

"Covellia Roxburghiana Miq."—Miquel's description (1867) 3: 270 of *F. triloba* included a reference to specimens from the Khasia Mts. and from Sikkim which had been collected by Hooker f. and Thomson. He spoke of large ovoid figs, and said that the flowers were like those of *F. hirta*. In the herbarium of the New York Botanical Garden are two specimens labeled *Covellia Roxburghiana* Miq. Both are from the collection of Hooker f. and Thomson. One is from the Khasia Mts. and the other from Sikkim. The first has cordate unlobed blades 13-18 x 4-12 cm., and is almost exactly like Wight's plate of *F. hirta* Roxb. The Sikkim specimen has the same kind of unlobed leaf and also a 5-lobed one about 24 x 24 cm., almost the same as in Wight's illustration of *F. hirsuta* Roxb. except that the central lobe, being broken, can not be compared. A petiole is 14 cm. long. The fig is ovoid, 4 x 2.5 cm., with a protruding apex like that in Wight's plate of *F. hirta*. The twigs are thick like those of *F. fulva*. A third specimen, labeled var. *Roxburghii* and collected in Sikkim, came from the herbarium of Otto Kuntze. It has 3- and 5-lobed leaves to 30 x 22.5 cm., but no figs. It appears to be *F. fulva*.

F. triloba according to Kurz.—The detailed description of *F. triloba* and *F. hirta* Vahl in British Burma, made by Kurz (1877) 2: 449-450, differ from each other principally in the brown, less hispid hairiness of the former, its sometimes long (10 cm.) petioles, its rather larger blades (15-30 cm.), and

its larger basal scales (6-8 mm.) of the receptacle. The hairiness of *F. hirta* is said to be gray as a rule, although both species may have tawny hairs. The figs vary in size from that of a small cherry to 1.3 cm. in *F. triloba*.

If these descriptions are of two different species they may refer to *F. fulva* and *F. hirta*. Or they may both belong to the variable *F. hirta*. The receptacles of Kurz' *F. triloba* do not show the large size of var. *roxburghii*, but are described as turbinate-globose, the shape of the smaller, female figs.

Var. *roxburghii* in Indo-China.—Gagnepain (1928) 5: 803-804 and in keys seemed to conceive of *F. hirta* as having always unlobed leaves, and of var. *roxburghii* as possessing always lobed ones. He cited specimens of the latter by collectors and places, but not by numbers. Three specimens in NYBG labeled var. *roxburghii*, from locations in Indo-China and collectors named by Gagnepain (*Poilane* 10912, 13049; and *A. Chevalier* 1137) have too small leaves and figs to belong to that variety. *A. Petelot* 3578 has a leaf like that of Hooker & Thomson's from the Khasia Mts., and a fig only 8 mm. in height when dry.

Var. roxburghii in China—Léveillé's *F. esquiroliana* and its synonyms *F. laus-esquirolii* and *F. neo-esquirolii*, all from China, have been identified by Rehder (1929) 10: 127 as var. *roxburghii*. And Handel-Mazetti (1929) 7: 99 has reported very large lobed leaves of *F. hirta* from SW China.

"Var. *roxburghiana*" Cowan & Cowan.—Both *F. hirta* and var. *roxburghiana* were listed by these authors from N. Bengal; the latter without description.

SUMMARY OF VAR. ROXBURGHII

This variety, according to King, resembles *F. hirta* Vahl in shape of leaf-blade and in figs, and in its flowers. It is like *F. fulva* in its type of hairiness and in size of leaf and receptacle. It varies from both these species in its distribution.

The forms making up the *roxburghii* group as characterized by Roxburgh, Wight, Kurz, and Léveillé seem to resemble one another and *F. fulva* more than they do *F. hirta*. Gagnepain's conception apparently is of var *typica*.

If King was correct in uniting all the above forms mentioned before his date this variety may be intermediary between *F. fulva* and *F. hirta*. If he was incorrect his form may be *F. hirta* var. ?, and the others may belong to *F. fulva*, perhaps to an unnamed variety.

There is no possibility that the *roxburghii* group should be allocated to the species usually known as *F. roxburghii* Wall., which differs in leaf and fig.

FICUS FULVA VAR. MINOR King, Ann. Bot. Gard. Calcutta 1: 149. pl. 187-2. 1888.

The problem of this variety seems to be whether things which are declared equal to the same thing are really equal to one another. It may be stated more specifically as follows: is this variety the same as *F. chrysocarpa* Reinw. ex Blume, and is that the same as *F. aurata* (Miq.) Miq.?

King's text differentiated var. *minor* by its ovate or elliptic leaves from the typical form, which, he said, had rounded, more or less lobed leaves. His plate shows an obovate blade 14.5 x 7.5 cm. in size, with an abrupt, very short and thick acumen and a narrowed base. It is unlobed and the margin is entire, or slightly wavy. There is one pair of basal veins which runs ¾ of the way to the apex. Four pairs of lateral veins are connected by transverse veinlets. The thick petiole is 1 cm. long. The figs are globose-ovoid, about 1.5 cm. in diameter, sessile, apiculate, and hairy. A bud is 1.5 cm. long, narrow-ovate, and acuminate. The location was not stated.

Synonyms cited by King were *Pogonotrophe flavidula* Miq. and *F. chlorocarpa Miq.* The second, according to the page reference given by King, should have been *F. chloroleuca* Miq. which, as has been said above, is a synonym of var. *typica* through its synonymy with *F. apiculata* Miq. 1854. The first synonym was described from W. Sumatra and has been accepted as belonging to var. *minor* by Koorders & Valeton and others.

Pogonotrophe flavidula Miq. added to King's description or changed the following characters: twigs, petioles, and nerves especially on under surface, short-bristled, roughish, yellowish hairy to glabrous; petioles to 5 cm. long; blades ovate or oblong-ovate; base rounded or subround; margin toothed; buds subglobose; figs larger than a cherry pit; peduncles short, yellow-hairy.

Miquel in 1867 determined "*F. flavidula* Miq. under *Pogonotrophe* (1860)" as a synonym of *F. chrysocarpa* Reinw. ap. Blume, which, he said, was a more glabrous form with subentire leaves. Another synonym made by Miquel was *F. fulva Zollinger* 811 (although that had both lobed and unlobed leaves). On a later page of the same text Miquel narrowed the allocation to *F. chrysocarpa β flavidula.*

Koorders & Valeton (1906) 11: 37, 254, 255 spoke of var. *minor* as one of two forms of *F. fulva* in Java. They said that it had stiffer, more protruding hairs than the typical form, that the leaves were unlobed, entire, smaller and more obovate than the type, and that the base was more or less rounded or wedge-like. They believed that this variety was the same as *F. chrysocarpa.* Koorders (Exkursionsflora von Java, 117. 1912) called it *F. fulva* var. *chrysocarpa.*

H. O. Forbes (1925) 63 suppl. 110 mentioned var. *minor* from Java, giving the native name as "Seuhang," as Koorders & Valeton had done in discussing *F. fulva.*

Gagnepain (1928) 5: 805 recorded var. *minor* from Indo-China. He listed slenderer twigs than those of the typical variety, 3-4 perianth parts in the female flowers instead of the 5 given by King for the species *F. fulva,* and spoke of the location of these flowers "among long yellow silks" (transl.). (The last two characters are those of *F. aurata.*) Gagnepain cited, by collector and place but not by number, specimens of var. *minor* from Tonkin and Annam. One in NYBG which agrees well with his description is *Poilane* 7866, from Annam. It is apparently the same as some other specimens from Sumatra and Annam which are labeled *F. hirta* Vahl, but which may be *F. aurata.* One from Tonkin is about the same. Gagnepain thought that another

with lobed leaves like *F. hirta* var. *roxburghii* might be a hybrid. Perhaps this was *Poilane* 10822 which has large figs and seems to be *F. fulva* var. *typica*.

F. chrysocarpa Reinw. ex Blume.—King would not have agreed with the assertion of Koorders & Valeton that *F. chrysocarpa* was his var. *minor*, for on pp. 151-152 and on pl. 191 he described and pictured what he thought was Reinwardt's species. Synonyms cited by him were *F. arguta* Wall., *F. densiserra* Miq., *Covellia aurata* Miq., and *F. aurata* (Miq.) Miq. These may be called for convenience the *aurata* group, since Miquel had placed the second name as *β densiserra* under *F. aurata*, his later version of *Covellia aurata*, and Kurz, according to Miquel, in letters had allocated *F. arguta* to this group.

Koorders & Valeton, of course, vigorously dissociated *F. chrysocarpa* from *F. aurata*, saying that the leaves had the same form but that those of *F. aurata* had much stronger teeth and long golden hairs, and that the figs were smaller, stiff-haired and peduncled. They declared that the species was near *F. hirta*, and that King at first allocated many Javan specimens to *F. hirta*, but later to *F. chrysocarpa*. Between the two were others which he called *F. fulva*. Their description of the figs is incorrect, according to the accounts by other writers.

F. chrysocarpa has been reported, by a few writers, from the Malay Peninsula, Indo-China, and the Philippines. Its problem has more phases than its possible relation to *F. fulva* var. *minor* and to *F. aurata*, and can not be decided definitely without additional knowledge as to the type specimen which would tell whether King's *F. chrysocarpa* is Reinwardt's.

However, at least some parts of *F. chrysocarpa's* problems seem solved. King's description is a sort of paraphrase of Miquel's of the *aurata* group, but with some important additions. He emphasizes, as Miquel and Gagnepain do, dense hairiness of the perianth parts and pedicels of the gall and female flowers. This seems to be quite a unique character. Certainly it was not reported for *F. fulva* or var. *minor*, *F. hirta*, or *F. chrysocarpa*, with the exception of Gagnepain for var. *minor;* although his account of that form differed from his of *F. chrysocarpa*. *F. hirta* is barred out also because *F. chrysocarpa* is described from Blume on as having no lobed leaves. The pubescence, too, is soft, instead of bristly.

Blume's account of *F. chrysocarpa* mentioned no hairiness on the leaves, although other writers have listed that. He spoke of rough twigs, and of ovate blades 10-16.3 x 5.5-9.5 cm., with a roundish base, a finely toothed margin and a rough upper surface. The receptacles were cherry-like, subsessile, and tomentose. According to the specific name they were golden in color. The native name was Kondang Kuning. King pictures a leaf about the size of that of var. *minor*, but with a more slender acute apex and a rounded instead of a narrowed base. The margin is finely serrate, the basal veins are shorter and the lateral veins are more numerous. Petiole and ovoid fig seem like those of var. *minor*, but the flowers have only four perianth parts. Other writers such as Miquel (1859) 1[2]: 302 and (1867) 3: 270, and Kurz (1877) 2: 450 name characters of *F. chrysocarpa* which seem to bring it and var. *minor* closer together, such as obovate leaves and an almost entire margin. It will be

remembered that *P. flavidula*, which King chose as a synonym of var. *minor*, was determined by Miquel as a variety of *F. chrysocarpa*.

The preceding paragraph is an argument for the identity of var. *minor* with *F. chrysocarpa* and also for the identity of King's species of that name with Blume's (Reinwardt's).

Specimens labeled *F. chrysocarpa* and *F. hirta* provide additional information. Quisumbing (Philip. Jour. Sci. 41: 317. 1930) reported *F. chrysocarpa* as new to the Philippines and cited *Ramos & Edaño* 49913 as an example. To this Sata (1944) pt. II: 357 added *G. Edaño* 77382.• No. 49913 (in NYBG) agrees well with *F. aurata*, even to the hairy interior of the fig; but no. 77382 has ovate leaves 37 x 23 cm. in size and also 3-lobed leaves almost as big. Another specimen of the same number at BH has only a 3-lobed blade. *G. Edaño* 77425, labeled *F. chrysocarpa*, has large ovate leaves and large figs, both like those of *F. fulva* var. *typica*. The following, labeled *F. hirta*. also show hairy interiors in their receptacles: *Toroes* 4337, *Posthumus* 685, and *Otto Kuntze* 6116. It must be admitted, however. that some other specimens, apparently of the same species, do not contain "silks."

Finally, Dr. E. D. Merrill in a recent letter speaks of a leaf from the Leiden collection, collected in Borneo in 1857-1861 by De Vriese, and labeled *Ficus chrysocarpa* (*F. aurata* Miq.) He noted that other specimens in the Leiden Herbarium were so labeled. This may be the specimen of *F. aurata* collected by De Vriese in Borneo to which Miquel referred in (1867) 3: 271, speaking of its hairy perianth.

CONCLUSIONS CONCERNING F. FULVA VAR. MINOR

This study postulates, partly in the hope of further investigation by others, that *F. fulva* var. *minor*, *F. chrysocarpa* Reinwardt ex Blume, and the *F. aurata* group are synonymous and form an independent entity with the earliest name, *F. chrysocarpa*. It asks, too, whether the flowers and fruits in the female receptacles always produce hairs. Therefore the following synonymy:

FICUS CHRYSOCARPA Reinw. ex Blume, Bijdr. 475. 1825

Ficus chrysocarpa Reinw. ex Blume, Cat. Gew. Buitenzorg 35. 1823. *Nomen nudum. F. arguta* Wall. Cat. no. 4489. 1831. *Nomen nudum. F. densiserra* Miq. Fl. Ind. Bat. Suppl. 173, 426. 1860. *Covellia aurata* Miq. *Ibid.* 175, 433. 1860. *Pogontrophe flavidula* Miq. *Ibid.* 176, 435. 1860. *Ficus flavidula* (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 270. 1867. *F. aurata* (Miq.) Miq. *Ibid.* 3: 271. 1867. *F. aurata* β *densiserra* (Miq.) Miq. *Ibid. F. chrysocarpa* β *flavidula* (Miq.) Miq. *Ibid.* 3: 291. 1867. *F. fulva* var. *minor* King, Ann. Bot. Gard. Calcutta 1: 149. pl. 187-2. 1888. *F. fulva* var. *chrysocarpa* Koorders, Exkurs. Java 2: 117. 1912.

Type: Reinwardt. Mts. of Java.

Distribution: Burma, Malaysia, Indo-China, Philippines.

SUMMARY OF F. FULVA AND F. HIRTA

As compared with *F. hirta* var. *typica*, the typical form of *F. fulva* may be taller, with thicker twigs, long petioles and larger roundish or broad ovate lobed and unlobed blades. The blade base is cordate or rounded instead of

bulbous, and the lobes may be lower in the blade and less erect. The basal veins give the appearance of several sets. The figs are large. The flowers have 3 or 5 perianth parts. The pubescence is softer and less rough.

F. hirta is much more variable than *F. fulva*. It seems probable that *F. hirta* var. *roxburghii* belongs to the latter species, and that vars. *hibiscifolia* and *palmatiloba* should be allocated to *F. simplicissima* Lour. *F. fulva* var. *minor* seems to belong to *F. chrysocarpa* Reinw. ex Blume, which includes the *aurata* group.

There is need for an investigation of female receptacles of unlobed specimens of *F. hirta* (so labeled) and of *F. chrysocarpa* in order to discover the extent of hairiness.

FICUS HISPIDA L.f. Suppl. Pl. 442. 1781

This species presents certain almost unique distinguishing characters, but also others which show such variability that they have given rise to a large number of synonyms. It is possible, too, that the descriptive and well-known specific name *hispida* should be supplanted by one less desirable from most points of view.

The unique characters are the almost invariably opposite leaves and the large, peduncled figs which usually grow on thin whip-like leafless twigs springing from the trunk of the tree or from the main branches. The multiplicity of synonyms is due principally to variations in the arrangement, margin, surfaces, and size of the leaves; and to differences in the location, arrangement, surface, and number of the figs, and the presence or absence of their peduncle. It is significant that differences which originally led to the creation of many species now are considered unworthy to differentiate varieties.

Ficus hispida is an example of the sub-genus *Covellia*, which is characterized in part by the position of some or most of its receptacles on long leafless branches which come from near the base of the plant and may trail upon the ground or even continue growth beneath the surface.

SYNONYMY

[*Perin teregam* (*Perim-teregam*) Rheede, Hort., Mal. 3: 81. pl. 61. 1682]. [*Ficus malabarica foliis asperis major, fructu itidem rotundo, lanuginoso majore* Ray, Hort. Pl. 2: 1435. 1688]. *Ficus peru teregam* L. ex J. Burm. Ind. Univ. in Rumph. Herb. Amboin. 6: (no p.) 1755. *F. hispida* L.f. (above). Not Roxburgh or Blanco. *F. simphytifolia* Lam. Enc. Méth. 2: 498. 1788. *F. sycomorus* Lour. Fl. Coch. 664. 1790. Not L. *F. amara* Noronha, Verh. Bat. Gen. 5: art. 4: 15. 1790. *Nomen nudum. F. scabra* Jacquin, *Plantarum rariorum horti caesarei schoenbrunnensis* 3: 36. pl. 315. 1798. Not Blanco, Forster f., Kunth, Sim, Willd, or Australian botanists. *F. oppositifolia* Roxb. Pl. Cor. 2: 14. pl. 124. 1798. *F. mollis* Willd. Act. Acad. Berol. 1798, 103. pl. 5. 1801. Not Miquel or Vahl. *F. daemonum* Koenig ap. Vahl, Enum. Pl. 2: 198. 1806. Not Zollinger. *F. fecunda* Blume, Cat. Gew. Buit. 36. 1823. *F. prominens* Wall. Cat. no. 4537. 1831. *Nomen nudum*. As synonym. *F. pilosus* Hb. Russel ex Wall. Cat. no. 4538 D. As synonym. Not *F. pilosa* Reinw. ex Blume, King, or Naves. *Gonosuke scabra* (Jacq.) Raf. Sylv. Tell. 58. 1838. *G. hispida* (L.f.) Raf. *Ibid. G. demonum* (Koen. ap. Vahl) Raf. *Ibid. Sycomorphe roxburghii* Miq. Ann. Sci. Nat. III, 1: 35. 1844. *Covellia scabra* (Jacq.) Gasp. Nov. Gen. Fic. 11. 1844. *C. oppositifolia* (Roxb.) Gasp. Ric. Capr.

85. pl. 8, f. 36-42. 1845. *F. toxicaria* Hb. Madr. ex Miq. Hook. Lond. Jour. Bot. 7: 461. 1848. As synonym. *C. hispida* (L.f.) Miq. *Ibid.* 7: 462. *C. setulosa* Miq. *Ibid.* *C. daemonum* (Koenig; Vahl) Miq. *Ibid.* *C. courtallensis* Miq. *Ibid.* 7: 463. *C. wightiana* Miq. *Ibid.* *C. assamica* Miq. *Ibid.* 7: 464. *C. dasycarpa* Miq. *Ibid.* *F. repens* Hook. Hb. ex Miq. *Ibid.* 7: 465. As synonym. Not Gardeners Chronicle, Hamilton, Miquel (1848) 7: 229, Rottler, Wallich, or Willdenow. *F. lima* Hb. Royen ex Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 282. 1867. As synonym. Not Schumann & Lauterbach. *F. sambucixylon* Lévl. Fedde, Repert. Spec. Nov. 9: 444. 1911.

Variable evergreen or partly deciduous tree 5-12 or to 17 m. high, or shrub usually 2-4 m. high; trunk straight, branching near ground, no aerial roots or buttresses; bark thin gray or greenish or tan, bristly with pale or brown hairs, becoming bare, rough, scurfy, and eventually peeling in irregular flakes, sometimes horizontal ribs around trunk; twigs 5-10 mm. in diameter, bearing conspicuous stipule and petiole scars; buds to about 2 cm. long, narrow ovate, stipules more or less persistent, triangular-acuminate, pubescent; leaves almost always oppositely arranged; petiole 1-7.5 or 10.5 cm. long, thick, hairy or bristly to scurfy; blades membranous, brittle when dry or sometimes leathery and stiff; ovate, elliptic or obovate, sometimes inequilateral; 6.5-30 or 40 x 2.5-15 or 20 cm. (examples: 8.5 x 4, 12 x 8, 18 x 6.5, 30 x 12.5); apex usually narrowed then rather abruptly acuminate, acumen 1-2 cm. long, slender or thick; base usually rounded or sub-cordate, sometimes obtuse, narrowed or broad-cuneate; margin cartilaginous, entire, undulate or shallow-toothed; upper surface usually rough with papillae, each bearing a stiff hair, sometimes becoming bare with papillae conspicuous as white dots or almost invisible, rough like sandpaper; lower surface soft- or stiff-hairy, especially along the largest veins; midrib continuous; basal veins about the thickness of the lateral veins and almost parallel to them, one large pair and about two smaller pairs (really branches of the largest one); usually 5-7 sets of lateral veins, upper angle at midrib 40°-50°, but soon curving up, not forking near margin, but connecting with nearest laterals by thickened transverse veinlets; transverse veinlets at angle of about 90°, sometimes broken or forked; no marginal vein; receptacles occasionally axillary and paired, commonly on leafless rope-like or branched twigs to 1 m. long (examples: 38, 45 cm.), which hang from the trunk and sometimes from the main branches, and occasionally trail on or under the ground; receptacles pyriform or globose, 1-3.5 cm. broad by 1-2.5 cm. high when fresh; apex depressed or truncate when mature, bearing several bracts which may form an annular ring; base rounded or narrowed into a neck above the peduncle; surface pubescent or hispid, sometimes appearing pebbly, warty, or woody, light green with longitudinal dark stripes, becoming yellow or yellow-green, sides sometimes fluted; basal bracts 3, forming a collar or disk at the base of the neck or at its apex; lateral bracts sometimes present on the sides of the receptacle; peduncle 5-15 mm. long, rarely absent, hispid; perianth of female flowers said to form a cup around the ovary, style hairy.

Type: Thunberg. Java.

Distribution: India and native states north of it, Ceylon, Burma, Andaman Islands, Malaysia, Indo-China, Siam, southwest China, Australia. Planted in other continents; examples in U.S.: Los Angeles, Miami, Kauai, and Oahu.

Uses: Ropes made from bark fiber. Bark and fruit medicinal: fruit crushed and

mixed with salt water used to treat diarrhoea. Leaves used for polishing and for elephant fodder. Trees furnish wood and shade for coffee plants.

Common names: Opposite-leaved fig-tree. Rough rubber tree. Devil's fig. Stiff-haired fig. Milk tree.

References for descriptions and illustrations: Corner (1933) 11: various pp. and plates. Gagnepain (1928) 5: 810. Haines (1924) 5: 837. King (1887-1888) 1: 116-117. pls. 154, 155; (1888) 5: 522. Koorders, in Teysmannia 11: 573-575. 1901. Koorders & Valeton (1906) 11: 208-212; (1918) pl. 766, 767. Wight (1843) 2: pl. 638, 641. Also standard books on Indian, Malayan, and Australian species.

Specimens (examples at NYBG, BH, or AA): *M. R. Henderson* 23132, *Holttum* 24575, from Malay Peninsula. *Poilane* 8818, 13564 (Indo-China). *Koelz* 8271 (India). *H. Y. Liang* 63275, 66231 (Hainan). *U.S.P.I.* nos. 101339 and 139365 probably are *F. hispida. Living trees:* CF, FTG, & Miami.

The authorship of *F. hispida* has been ascribed to Thunberg, who was the collector named by Linnaeus f. and may have suggested the specific name, since his own descriptions (1786) 6, 13 cited no author for *hispida;* also to Linnaeus; to Lamarck; and to Blume, on the theory that Blume's *F. hispida* differed from that of Linnaeus f. *F. hispida* Roxb. is *F. hirta* var. *roxburghii* (Miq.) King or *F. fulva* Reinw. ex Blume; and *F. hispida* Blanco is *F. ulmifolia* Lam.

EVALUATION OF SYNONYMS

A flood of synonyms began about seven years after the first publication of *F. hispida* and continued through the time of Miquel with comparatively few mentions of the name given by Linnaeus f. In (1867) 3: 296 Miquel, who had been responsible for many of the synonyms, assembled his own and several others under *F. hispida.* King added somewhat to the list. The synonymy in this study includes a few more names which have been vouched for by other botanists. Rafinesque's genus *Gonosuke* now has disappeared. *Covellia* of Gasparrini and Miquel has been retained as a sub-genus of *Ficus* in which the receptacles are borne on long leafless twigs and contain either male and gall flowers, or female flowers.

A contributing cause to the great number of synonyms was the insufficient description by the younger Linnaeus, who apparently was so impressed by the universal bristly hairiness that he omitted decisive characters of arrangement and size of leaves and figs. Through Thunberg the picture of the species was enlarged to include long petioles, large rough and serrate blades, and big axillary and racemose receptacles. Opposite leaves as a character appeared in 1798. The following Key has been made to show characters which the *original* descriptions of the synonyms indicated were distinctive.

KEY

1. Figs sessile.
   2. Blades to 5 cm. long, margin toothed, under surface bristly; figs bristly to bare ..... *F. sambucixylon*
   2. Blades more than 5 cm. long, margin entire or wavy, under surface soft-hairy; figs hairy ..... *F. mollis*
1. Figs peduncled or not characterized.
   2. Figs axillary or not characterized.

3. Blades lanceolate-oblong or sub-lanceolate, base acute, arrangement both opposite and spiral. Assam ..... *C. assamica*
3. Blades "oblong."
4. Leaves opposite, rough above, soft beneath; figs villose, cherry-like. East Indies ..... *F. daemona*
4. No arrangement mentioned, leaves hairy; figs hispid, globose. Java. ..... *F. hispida*
2. At least some figs in clusters or/and on leafless fruiting branches.
3. Leaves spirally arranged or not characterized.
4. Blades entire, ovate, subcordate, wood showing some red.
5. Leaves bearing fine rigid spines. Malabar, India ..... *Perin teregam*
5. Leaves tomentose beneath. Cochin China ..... *F. sycomorus* Lour.
4. Blades toothed; twigs rough and hairy.
5. Largest blades not more than 14 cm. long, rough-hairy above, softly hoary-hairy beneath; figs obovate turbinate ..... *C. dasycarpa*
5. Largest blades more than 14 cm. long, rough on both surfaces, stiff-hairy; figs globose ..... *F. simphytifolia*
3. Leaves oppositely arranged.
4. Under surface of blade downy, margin toothed; twigs hollow ..... *F. oppositifolia*
4. Under surface of blade bristly or rough.
5. Figs growing from trunk; blades toothed ..... *F. scabra* Jacq.
5. Figs axillary or on leafless twigs or branches.
6. Base of blade slightly narrowed, blades to 20 cm. long ..... *F. setulosa*
6. Base of blade rounded, blades more than 20 cm. long ..... *C. wightiana*
6. Base of blade subcordate.
7. Figs pubescent, racemes buried in ground; blade surfaces papillate, mostly soft-hairy, margin toothed or entire. India ..... *C. courtellensis*
7. Figs hispid; blade surfaces scabrous, margin toothed ..... *F. fecunda*

Ficus peru teregam derived its name from the species which was called *Perin teregam* in Rheede's text and *Perim teregam* on his plate. J. Burman, editor of *Herbarium Amboinense* by Rumphius, in his comment on *Caprificus viridis* Rumph. (1743) 3: 151-152 had said that "*Peru Teregam*" Rheede was certainly *C. viridis*. In a dissertation on *Herbarium Amboinense* presented May 9, 1754 under the asserted authority of Olaf Stickman, but generally credited to Linnaeus, the equivalent of *Caprificus viridis* was given, with a question, as "Ficus Peru Teregam H.M. 3, t. 61?," the reference being to Rheede's *Hortus Malabaricus*, vol. 3, plate 61. Although this name was not published until the dissertation was printed in *Amoenitates Academicae* 4: 124. 1759, J. Burman referred to it in 1755 in the appendix to the 6th volume of Rumphius' text, calling it *Ficus Peru teregam* H.M.L. But in 1769 Burman omitted it from his index to Rheede's volumes.

Caprificus viridis major has been identified by Merrill (N.1917) 195 as *F. conora* King and is of no further significance as regards *F. hispida;* but Rheede's species and the names growing out of it have been both accepted and repudiated as synonyms of *F. hispida* or of certain of that species' synonyms.* The resemblances to *F. hispida* as shown in Rheede's text and plate are: color and surface of bark; size, shape, surface and veining of blade; size and shape of receptacle and their arrangement singly or in clusters on long leafless

* For a summary of many allocations see J. K. Hasskarl, Hort. Mal. Clavis 29. 1867, reprinted from Nov. Act. Leop.-Carol. Deutsche Akad. Nat. 33. 1867.

branches. Differences from the most common phases of leaves and figs are the spiral arrangement of the leaves, the short petioles, the wavy and toothless margin of the blades and the lack of bracts of the figs. In rebuttal it may be said that King has illustrated alternately arranged leaves and that Miquel said that his *Covellia dasycarpa* seemed to be forma *alternifolia* of *F. hispida*. Petioles 1 cm. long are to be seen in specimen *Wang* 33464 from Hainan, and entire margined leaves were collected by me from a tree of *F. hispida* at 4921 SW. 13th St., Miami. The dry leaves are very apt to have curled under at the margin. Basal bracts, however, usually are conspicuous. Rheede's common names, whose translations are tall file- or rasp-tree, seem appropriate.

Although I believe that *Perin teregam* is the prototype of *F. hispida* and that a correctly spelled version of it should be the valid specific name of that species I am more than willing to accede to the doubts expressed by authorities and to retain the simple and suitable title given by Linnaeus f.

F. symphytifolia, as it usually is written, was described by Lamarck from a Javan, or at least East Indian specimen. Lamarck said that Rheede's plate would have represented his plant well enough if it had shown toothed leaves. He mentioned also *F. hispida*, but made only a translation from Linnaeus f. King (1887-1888) 1: 184 cited it as a probable synonym of *F. hispida*.

F. sycomorus Lour. from Cochin China has been determined as *F. hispida* by Merrill (Je. 1935) 24[2]: 137.

F. amara Noronha, reported without description from Java, has been suggested as a possible synonym by Miquel and King.

F. scabra Jacq. was a shrub in the Imperial Garden at Schoenbrunn near Vienna. Persoon (1807) 2: 611 linked it with *F. hispida* and it has been cited often for that species or one of its synonyms. Merrill, however, (Jour. Arnold Arb. 23: 158. 1942) says Jacquin's plate is not of a *Covellia*.

F. oppositifolia was described by Roxburgh from the Coast of Coromandel, on the southeastern shore of India. It was illustrated also by Wight, and, from Assam, probably also by Griffith (1854 a) pl. 560. Willdenow, who liked appropriate names, chose this title in preference to *F. hispida*, and has sometimes been considered its author. *F. oppositifolia* seems to have been the most popular name for the species until the time of Miquel.

F. mollis Willd.—This name has been reported as published in 1798. I have examined only an apparent reprint in Koenig & Sims, Ann. Bot. 2: 324. pl. 12. 1806. It was cited by Willdenow (1806) 4: 1151 as a synonym of *F. oppositifolia*, and has been accepted for *F. hispida* by Miquel and King.

F. daemonum was the name given and probably described by Koenig, who reported it from the East of India or the East Indies. It was published by Vahl. According to Baillon, *Histoire des plantes* 6: 176. 1877 the tree was poisonous. The incorrect termination of the specific name was corrected by Roxburgh (1814) 66, who listed the species as a shrub introduced into the Calcutta Garden from Tanjore in southeastern India. Roxburgh sometimes

has been called the author of the name, as have also Roth, and Wight, who illustrated it. This illustration shows lateral bracts and an underground fruiting branch such as is mentioned in notes by Roxburgh (1932) 3: 563. It has been allocated to *F. hispida* and to many of its synonyms.

F. fecunda Blume (1823) was declared a synonym of *F. hispida* L.f. by Blume (1825) 470. and by Miquel (1867) 3: 296.

Synonyms from Wallich.—*F. prominens* Wall. no. 4537 was allotted to *F. hispida* by King, and has been accepted by Koorders & Valeton. All the 13 sections of *F. daemonum* Vahl in Wallich's catalog, no. 4538 were included under *F. hispida* by King. All sections except A, *F. oppositifolia* Hb. Wight; D, *F. pilosus;* and N, also from Hb. Wight, consisted of place names.

Gonosuke spp.—Rafinesque said that his names (in the synonymy above) had been united by Smith (J. E.) into *F. oppositifolia.*

F. scabra.—Gaspartini thought *F. scabra* might not be a *Covellia* because it had opposite leaves. This objection shows that *F. scabra* for which he cited no author was the species so called by Jacquin.

Sycomorphe roxburghii.—Miquel described this new genus as having axillary or racemose peduncled receptacles and opposite leaves, and cited *F. oppositifolia* of Willdenow and Roxburgh, and *F. macrophylla* Roxb. as synonyms. The latter, however, is *F. roxburghii* Wall. It is a question whether Miquel knew of Wallich's changing of the name given by Roxburgh, which had been preceded by the *F. macrophylla* of Desf.; Pers., or whether Miquel was honoring Roxburgh. In (1848) 7: 461 he wrote it as a synonym of *C. oppositifolia.*

F. toxicaria.—Miquel included this herbarium specimen among the synonyms of *C. oppositifolia.*

Covellia spp. of Miquel.—Miquel (1867) 3: 296 grouped his *C. setulosa, C. courtallensis, C. wightiana,* and *C. dasycarpa* as unnamed varieties of *F. hispida.* The first, third and fourth came from the East Indies, and the second from Courtallum, in southernmost India. A synonym cited for *C. dasycarpa* was the herbarium specimen *F. repens.* On p. 282 he had mentioned forma *borneensis,* with axillary figs, which had been collected in Borneo by De Vriese. *F. daemonum,* which Miquel had called *C. daemonum,* he listed as a synonym of *F. hispida. Covellia assamica,* a form with both alternate and opposite leaves, he seems to have overlooked in his summary of the species of *Ficus.*

F. sambucixylon Lev.—Apparently, since Miquel's day the only accepted new synonym of *F. hispida* is this one from China. The type is *J. Esquirol* 2217. Rehder has identified it as *F. hispida,* in Jour. Arnold Arb. 10: 126. 1929.

SUMMARY

Ficus hispida is one of two well-known species of figs which almost always have opposite leaves. In spite of this distinguishing character the other features of the leaves show such variability that many synonyms have accumu-

lated. None, however, is sufficiently distinctive to constitute a variety.

The earliest name for this species seems to be *Ficus perin-teregam*, which is derived from *Perin teregam* Rheede. It was incorrectly and doubtfully called *F. peru teregam* by Linnaeus, and was so quoted by J. Burman, with a reference to Linnaeus. Nevertheless, since the identity of *Perin teregam* Rheede with *F. hispida* has never been entirely acceptable, it seems better to continue the later and more descriptive name.

FICUS LACOR Ham.

The Indian Spotted Fig-tree is well known in Asia and, in its typical form and in var. *cunninghamii*, often has been cultivated in Florida. Its recognition there presents no difficult problem, since its thin ovate-elliptic deciduous leaves with rounded base and slender acumen, and its small whitish figs spotted with pink are quite characteristic; but its nomenclature is much involved with other species. In fact, it has no right to the name by which it is best known: *Ficus infectoria* Roxb. Its correct title, *Ficus lacor*, has been acknowledged for years, but has been used seldom, even by those who have recognized its validity.

Florida writers recommend this species with some reservations, because of the great spread of branches in mature trees.

FICUS LACOR var. TYPICA (King) M. F. Barrett, Amer. Midl. Nat. 36: 425. S1946 [Ja 1947]. (Authorship correction.)

F. infectoria Roxb. Hort. Beng. 66. 1814. *Nomen nudum.* Not Willd. 1806. ? *F. tsjela* Ham. Trans. Linn. Soc. 15: 149. 1827. ? Not Roxb. *F. lacor* Ham. *Ibid.* 15: 150. 1827. ? *F. venosa* Ham. *Ibid.* 15: 151. 1827. Not Aiton or Willd. *F. sp.* Wall. Cat. no. 4519 F. 1831. *Under F. venosa* Ait. *F. sp.* Wall. Cat. no. 4568. 1831. Under *F. subrepanda* Wall. *F. infectoria* Roxb. Fl. Ind. ed. 2, 3: 551. 1832. Not Willd. 1806. *Urostigma infectorium* (Roxb.) Miq. Hook. Lond. Jour. Bot. 6: 566. 1847. ? *U. timorense* Miq. *Ibid.* 6: 569. 1847. ? *F. terminalioides* Griff. Itin. Notes 2: 101. 1848. Ic. Pl. Asiat. pl. 550. 1854. ? *F. monticola* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 216. 1867. ? *F. timorensis* (Miq.) Miq. *Ibid.* 3: 286. 1867. *F. infectoria* forma *typica* King, Ann. Bot. Gard. Calcutta 1: pl. 75. 1887-1888. *F. infectoria genuina* Koord. & Val. Booms. Java 11: 140. 1906. *F. tenii* Lév. in Fedde, Repert. Sp. Nov. 6: 112. 1908. *F. infectoria* var. *typica* (King) Domin, Bibl. Bot. 89: 563. 1921.

A tree, becoming 12-17 m. high (example: 15 m.), often epiphytic, usually deciduous and bare for a short time; crown broad (example: 25 m.), dense; trunk short, thick and lobed when composed of epiphytic roots, light-colored, smooth with horizontally elongated lenticels, or cracked, or peeling in strips; often buttressed and bearing prop roots; branches horizontal, drooping at tip, sometimes bearing aerial roots which do not form secondary trunks; twigs 4-8 mm. in diameter, glabrous, greenish to brown; terminal buds ovate, 5-10 mm. high, stipules elongating with the leaves, then falling; leaves in 5 rows; petioles 2.5-7.5 cm. long, usually 4 to 5 cm., slender, glabrous; blades elliptic or oblong-ovate, 8-19 x 3.5-10 cm. (examples: 8 x 3, 13.5 x 6, 15 x 7 cm.); base usually rounded; apex gradually narrowed from below the middle to an abrupt acumen; acumen slender, acute at first, to 2.5 cm. long by 1 cm. at base; margin entire, usually crenulate when dry; both surfaces glabrous, the upper one glossy; young leaves paper-thin, pinkish at first, mature leaves thin, but rather

stiff when dry; one set of basal veins, sometimes with one or more basal branches, but parallel to the lateral veins and of about the same thickness; 7-11 sets of lateral veins, upper angle at midrib 60° to 70°, forked and confluent near the margin, making a deeply indented marginal vein; each intervein filled principally with two or more horizontal rows of large reticular spaces whose side walls slant and produce a herring-bone effect and whose end walls meet in a zigzag line or lines through the center of the intervein; smaller reticular spaces and checkered background present; receptacles axillary, typically paired, sessile or rarely very short peduncled, obovoid or globose, to 11-15 x 9-12 mm. when fresh and ripe, 6-10 mm. in diameter and corrugated when dry, glabrous, sometimes dotted, white flushed with pink, red, or orange when mature, but often dropping before maturity; apex sometimes raised; base narrowed; apical bracts 3; basal bracts 3, ovate, sometimes lobed, to 2-4 x 1.5-3 mm., puberulent to glabrous; male, gall, and female flowers together in the receptacle, variously described as sessile or stipitate; perianth of 3-5 usually linear sepals; one stamen, with a short filament; style somewhat lateral, stigma elongated, ovary in gall flowers longer than the sepals, in female flowers shorter.

Type: Of *F. infectoria* Roxb., *Roxburgh* coll. (?). East India Company's Botanic Garden, Calcutta. Of *F. lacor* Ham., Hamilton coll. District of Ganges, India. Said in Roxburgh (1832) to be a native of Bengal.

Distribution: Northern Peninsular India, Burma, Malaya, Indo-China, Formosa, China, Philippines. More often cultivated than wild, and probably not always native to places where it is so reported. Cultivated outdoors in the U.S.; in Florida, California, and Hawaii.

Common name: Spotted Fig.

Economic importance: Avenue and specimen tree, shade for coffee, wood used for timber and charocal, bark fiber for ropes, leaves for cattle and elephant fodder, young shoots eaten by man, decoction for gargle and mouth wash.

Illustrations additional to those in the synonymy: King (1887-1888) 1: pl. 84[52] (flowers), Mowry (1938) f. 42, Wight (1843) 2: pl. 665 (labeled *F. infectoria* Willd., but recognized by authorities as Roxburgh's species).

Descriptions and sometimes discussions: Beddome (1874) 2: 222, Cooke (1907) 2: 651, King (1887-1888) 1: 60-63 and (1888) 5: 515-516, Koorders & Valeton (1906) 11: 136-141.

Specimens: living trees (CF, FM, FTG, MCC, RPN); herbarium (BH) from Florida, *P.I.* 52406, 74592, *Moldenke* 5473; also from Hollywood, Los Angeles, San Diego, Santa Barbara in California; (NYBG) *J. G. Jack* 8671, *A. Petelot* 5258, *Y. Tsiang* 7238 [labeled *F. superba* Miq. (*F. tenii* Lev.) and *F. lacor* Ham.], and others.

ILLEGALITY OF THE NAME F. INFECTORIA Roxb.

Roxburgh (1814) cited no author of *F. infectoria*, although he referred to Rheede (1682) 3: pl. 64. He made no adequate description, saying only that this was a large tree which produced flowers in the hot season and figs in the rainy season. Native names were *Pakur* (Bengali) and *Plucsha* (Sanscrit).

The above paragraph shows that Roxburgh's title was non-valid. (1) His description was too slight to constitute publication. (2) Rheede's plate (incor-

* The tree illustrated in Rheede pl. 64 was described in the accompanying text as *Tsjakela*, but that spelling was corrected to *Tsjahela* in the *Index* and *Errata* which followed. Here the incorrect orthography of Burman and others is corrected. See M. F. Barrett, *Ficus tsjahela* in Bull. Torrey Club 73: 86-90. Ja 1946.

rectly labeled *Tsiela*, instead of *Tsjahela**), had already served as part of the basis for the valid species *F. tsjahela* Burm. f. (Flora Indica 227. 1768). Later, Rheede's form had also been called *F. venosa* by Aiton (1789) 3: 451, with no reference to Burman. (3) Willdenow (Hortus Berolinensis fasc. 3: 36. pl. 36. 1804) had described and illustrated as *F. venosa* Ait. a species with conspicuously light-colored veins. By 1806 he had found that his was a previously undescribed species, but he retained for it Aiton's appropriate name and re-christened [(1806) 4: 1137] *F. venosa* Ait as *F. infectoria*, with *Tsjahela* Rheede as another synonym. *F. venosa* Willd. of course was nonvalid, and was given the title *F. leucantatoma* by Poiret (1812). Merrill, (Contr. Arnold Arb. 8: 46. 1934) believes it is *F. septica* Burm. f.

Evidently Roxburgh (1814) thought that his *Pakur* was Willdenow's *F. infectoria*, and some other botanists* also have believed that Roxburgh's citation of *Tsjahela* showed that *F. infectoria* Roxb. was *F. tsjahela* Burm. f. But, although Roxburgh's notes published in 1832 credited his *F. infectoria* to Willdenow, they gave a very full description of a tree which differed decidedly from that named by Burman, Aiton and Willdenow. In short, Roxburgh (1814) inadequately described a new species under the illegal name *Ficus infectoria* Willd. of the tree *F. tsjahela*, and with the same reference to Rheede's plant which Willdenow had used. Nevertheless, in time the name *F. infectoria*, usually without the references cited by Willdenow, but sometimes with his name as author, came to represent Roxburgh's *Pakur*.

A third author was suggested when Blume (1823) 36 reported, without description, *F. infectoria* Reinw. from the botanical garden at Buitenzorg, Java. This was not included by Blume (1825) in his text on the plants of Java.

The stabilization of this species as *F. infectoria* Roxb. was due largely to King (1887-1888), although his text admitted that the name probably should be *F. lacor* Ham. King cleared up its history, prepared a synonymy, provided references and a new description and separated several varieties.

SUGGESTED SUBSTITUTES FOR "F. INFECTORIA Roxb."

F. lucescens Blume, Bijdr. 444. 1825, a tree growing on river banks near Buitenzorg, Java, is chronologically the first of the suggested replacements. The only characters distinguishing it from *F. lacor* are the small oblong-lanceolate leaves (5-11.5 x 1.7-4 cm.) and the short petioles (1.3-2.5 cm.). No figs are mentioned. According to Miquel (1867) 3: 265 *F. lucescens* was founded upon a sterile specimen which no longer was preserved in the local herbarium under that name.

Miquel (1859) 1[2]: 341 changed the title given by Blume to *Urostigma lucescens*. He reported the tree from the same locality and altered and added slightly to the description, but saw no receptacles. In (1860) 176 he hesitantly listed it from Sumatra. In (1867) 3: 264-265 he said that Blume's *F. lucescens* (but hardly his of 1859) perhaps was *F. infectoria* Roxb. His of

* Alston (1931) 6: 268, Robinson (1912) 7: 419.

1860 he gave as a questioned synonym of Roxburgh's form. But on p. 286 he accepted all three as synonyms.

King (1887-1888) cited *F. lucescens* Blume and *U. lucescens* Miq. as doubtful synonyms of *F. infectoria* Roxb., saying that he had seen no specimens and that the original description was too meagre and vague to be relied on. One or both names were accepted also by him in (1888), and by Gagnepain (1928) 5: 760, and others.

But Koorders & Valeton (1906) declared that *F. lucescens* Blume had been joined with *F. infectoria* by a mistake of Miquel's, and that the vernacular name *Loa*, mentioned by Blume, and an authentic specimen showed that it belonged to *F. glomerata* Roxb. On p. 269 they listed both *F.* and *U. lucescens* as synonyms of that species, and on p. 270 allocated them to *F. glomerata* var. *elongata* King. The correct name for this variety may be *F. racemosa* var. *elongata* (King) M. F. Barrett, Bull. Torrey Club 73: 323. My 1946. The narrow leaves of this variety and the large figs bear no resemblance to *F. lacor*.

On the other hand Alston believed that *F. lucescens* Blume with *F. lacor* Ham. as a synonym should supplant *F. infectoria* Roxb.

F. lacor was one of four Indian species discussed by Hamilton in 1827. The others were *F. tsjela* (p. 149), *F. scandens* ((p. 149), and *F. venosa* (p. 151-152). Most of them, he said, had the vernacular name *pakur*, or a similar title. For example, the Hindu and Bengali term for *F. lacor* was *lakor* or *nakor*. Specimens of three and perhaps four of these species, from Hamilton's herbarium, were listed in Wallich's catalog and were examined by King. He identified (pp. 62, 185) as *F. infectoria* Roxb.: no. 4519 D, labeled "? *F. infectoria* Hb. Hamilt." but placed by Wallich under *F. venosa* Ait.; no. 4520, *F. tsjela* Hb. Ham., which he said was a narrow-leaved form; and the first specimen of no. 4529, *F. lacor* Hb. Ham. " ? *F. scandens* Hb. Ham.," no. 4529 B, King determined as not *F. infectoria*, although Steudel (1840) 636 had listed that species as perhaps β under *F. lacor* Ham. Other allocations to Roxburgh's species, although not Hamilton's specimens, were no. 4519 F, from the Calcutta Botanic Garden; and possibly section A, *F. infectoria* Wight, and section C, " ? *F. venosa* Hb. Roxb.," of the same number; also no. 4568 B, an unlabeled specimen from Sylhet in Assam, placed by Wallich under *F. subrepanda* Wall.

Hamilton's text on these species accords quite well with King's determinations. The allocation of *F. tsjela* Hb. Ham. to *F. infectoria* Roxb. was confirmed by Haines (1924) 1248. Hamilton's description was too general to be assigned definitely to either *F. tsiela* Roxb. (more correctly known as *F. amplissima* J. E. Smith) or *F. infectoria* Roxb. If to the former, it would belong to the less common of two forms, because of a cuneate leaf-base. If to the latter, it is more likely to be var. *typica* than to be the form which King called var. *wightiana;* since Hamilton stated that the figs were sessile.

Hamilton accompanied his description of "*F. venosa* Poir" with synonyms and references belonging to *F. tsjahela* Burm. f. (*F. venosa* Ait., *F. infectoria* Willd.), but also cited *F. infectoria* Roxb. (1814), since he believed that his

form was different from *F. tsjahela*. He characterized it as having short petioles and twin figs. Miquel (1867) 3: 265, 286 thought that *F. venosa* Ham. was *F. infectoria* Roxb., and Haines (1924) 832 suggested that it might be a form of that species. King (1887-1888), however, placed it under *F. tsjahela*. *F. venosa* Voigt (1845) 287, although ascribed by Voigt to Aiton, refers to Roxburgh (1832) and obviously belongs to the latter's *F. infectoria*. If Hamilton's *F. venosa* is to be removed from the synonymy of *F. lacor* it should be replaced by Wallich's no. 4519 C of that name if that specimen is really *F. lacor*. If not, Voigt's *F. venosa* might be added to the synonymy.

Although Hamilton's description of *F. lacor* was incomplete it agreed well with Roxburgh's later one of *F. infectoria*, except in its character of white-hairy figs. However, King thought that this condition was abnormal and due to the attacks of insects, since Hamilton's own specimen, labeled *F. lacor* in his writing, was unmistakably *F. infectoria*. Trimen (1898) 63 and Cooke, as well as King, admitted that *lacor* had priority over *infectoria*, but cited the former as a synonym of the latter. Alston considered that *F. lucescens* preceded *F. lacor*, and Miquel cited it as a questioned synonym of *F. leucocarpa*. *F. lacor* has been employed as the specific name by Handel-Mazzetti (1929) 7: 92, Rehder (1929) 10: 124, and (1936) 17: 74, Steudel (1840) 636, Schneider* (1916) 3^2: 309, 310, and Wallich.

EVALUATION OF OTHER ALLEGED SYNONYMS

Placsha Jones, Asiat. Res. 4: 310. 1795.—This synonym was cited by Roxburgh (1832). Jones' description pointed toward *F. tsjahela* as to leaves and *F. lacor* as to figs. His rambling taxonomy referred also to a Linnean name for a species which may be *F. mysorensis* Heyne ex Roth. In any case this synonym is not in Latin form and is otherwise unimportant.

F. ampla Kunth, Ind. Sem. Berol. 18. 1846.—King (1887-1888) 1: 179 thought this might be *F. infectoria* Roxb. If so, it is not the typical variety, for it was described as having hairy twigs, buds, and leaves. The leaves measured 23.5 x 12-14 cm., and had petioles 2-4 cm. long. No figs were mentioned.

Miquel's proposed synonyms.—Four species which Miquel either originated or transferred from *Ficus* to *Urostigma* were cited by King (1887-1888) as synonyms of the present *F. lacor*.

F. infectoria Roxb. was transferred in 1847 to *Urostigma* and reference made to a specimen from Bengal in the herbarium of W. J. Hooker. Miquel reported the species also from the Netherlands East Indies in (1854) 90 and (1859) 1^2: 339. In (1867) 3: 264 and 286 this species and its reports were returned to *Ficus*. Credit is due Miquel for his separation (although a rather doubtful one) of Roxburgh's species from Willdenow's of the same name, for the checking of his own specimens with Wight's plate of "*F. infectoria* Willd.," and for the acceptance of *F. venosa* Ham. as a synonym. But he incorrectly, although hesitantly, appropriated the following as synonyms: *F.*

* In Sargent ed. *Plantae Wilsonianae*.

and *U. lucescens*, *F. subcalyptrata* Noronh. (which apparently was *nomen nudum*), and *U. ceylonense* forma *novella*. The species *U. ceylonense* now is conceded to be a synonym of *F. tsjahela* Burm. f. *U. aegeirophyllum* Miq. he accepted in 1867 on the authority of Thwaites, but made it a variety, β, under *F. infectoria*. This is considered a synonym of *F. lacor* var. *lambertiana* (below). It should be noted that King and some other authorities recognize Miquel (1859) as the source of *U. infectorium*, although Thwaites refers to Miquel (1847).

U. timorense was founded by Miquel on an herbarium specimen of Hooker's from Timor, and in 1867 was changed to *F. timorensis*. The latter name had already been applied to a different species by Decaisne. Miquel, however, eliminated Decaisne's species as an independent entity by transferring it as a synonym first to the typical variety of his own *U. accedens* and then in 1867 to *F. superba* (Miq.) Miq. as a synonym with *U. accedens*.

King cited *U. timorense* and *F. timorensis* (Miq.) Miq. as synonyms of *F. infectoria* Roxb., saying that Miquel had based the former upon a single specimen, but that he himself had seen the type in the Kew Herbarium and had decided that it was the typical *F. infectoria*. Later, (1887-1888) 1: 185, he asserted that probably it was *F. infectoria* var. *caulocarpa* (Miq.) King. This seems impossible from the description, which suggests rather that the *timorensis* forms may be var. *typica*, or that which King called var. *wightiana*. Koorders & Valeton and Gagnepain accept one or both forms for *F. infectoria*.

U. leucocarpum Miq. was described by Miquel (1847) 6: 576-577 from specimen no. 1914 in Wight's herbarium, which had hairy young parts and a peduncled ovate fig covered with white pubescence. He accompanied the name with a parenthesis containing the title *F. lacor* Ham., its source, and a question mark; and added "quo teste huc Wall. n. 4549," thus referring to the specimen which King later identified as *F. infectoria* Roxb. In (1867) 3: 285 Miquel transferred *U. leucocarpum* to *Ficus* and cited "*F. lacoor* Ham." as a questioned synonym.

King declared that Miquel had named *U. leucocarpa* from Hamilton's specimen (a statement which seems incorrect, from Miquel's text), and that Miquel also had attached the name to specimens which were like *F. chittagonga* Miq. Although the *leucocarpa* forms were cited by King and by Koorders & Valeton under *F. infectoria* Roxb. they seem, according to the above hint and their description, to belong to *F. glomerata* var. *chittagonga* (Miq.) King; or, more correctly, to constitute forma *chittagonga* of *F. racemosa* L. (See M. F. Barrett, My 1946, above).

F. monticola Miq. from the Khasi Hills in Assam was said by its author to be near *F. infectoria* Roxb. and *F. aegeirophylla*. The latter name was not validly published because it did not refer to the original title, *U. aegeirophyllum* (a synonym of *F. lacor* var. *lambertiana*). The description of *F. monticola* agrees better with var. *typica* than with var. *lambertiana*. King (1887-1888) 1: 182 cited it as probably *F. infectoria*.

"*F. tjiela* (not of Roxb.) Zoll. Cat. 3420" is listed by King (1887-1888) among the synonyms of *F. infectoria*. But that number is labeled *U. infector-*

ium and does not *mention F. tjiela.* Possibly King had in mind no. 4520 of Wallich's catalog, labeled *F. tsjela* Wall. (above). It will be noted that this specific name, which should be *tsiela,* is often spelled with the alternate *j* for *i,* and with the *s* omitted.

Griffith's species.—A species which Griffith (1854 a) named *F. terminalioides* on his plate 550, and *F. terminaloides* in his text (4: 393) was first described by him under the former name in 1848. It was a Formosan tree whose characters were similar to those of *F. lacor,* so far as the description went. The plate, however, showed an ovate leaf with a shape more like var. *lambertiana.*

King in both of his texts and Koorders & Valeton cited the 1854 plate as a synonym of *F. infectoria* Roxb. King (1888) cited both plate and text of 1854. The latter referred to the volume of 1848.

Léveillé's species.—Three Chinese species of Léveillé's were allocated to *F. lacor* by Rehder (1929) 10: 124. However, in (1936) 17: 74 he cited only one, *F. tenii* Lév., as a synonym, in company with *F. superba* (Miq.) Miq.

Of the three species of Léveillé's *F. tenii* obviously is the only one which resembles *F. lacor.* Two holotypes and one specimen in the New York Botanical Garden herbarium show that it is var. *typica* beyond a question. The holotypes were made from specimens in the garden of the University of California, and in Léveillé's herbarium at Edinburgh. The type is that of *Simeon Ten* 733.

The determination of *F. tenii* as synonymous with *F. superba* was made by Handel-Mazzetti (1929) 7: 92 and was denied by Rehder (above), but later accepted by him. *F. superba* has been linked with King's alleged variety of *F. infectoria, wightiana,* but differs from that form in greater hairiness (see below). That and its pedunculate receptacles separate it from *F. lacor* var. *typica.*

The other species made by Léveillé, *F. fecundissima* Lév. & Vant. and *F. pseudo-religiosa* Lév. bear no resemblance to *F. lacor* that I can see, judging by a few specimens in New York. They have tiny and very numerous figs, somewhat stipitate and also peduncled, with flaring bracts between the stipe and the peduncle. The veining of the leaves is very different from *F. lacor.* The leaves of *F. fecundissima* are rather like small ones of that species, but have a bent-back acumen. Those of *F. pseudo-religiosa* may be oblanceolate. Both leaves and figs are much smaller than those of *F. lacor.* These trees agree with no reports of alleged varieties and seem too different to belong to the species at all.

ALLEGED VARIETIES

Very few varieties of *F. infectoria* Roxb. or of *F. lacor* were suggested before King's time: perhaps only those proposed by Steudel and by Miquel (see above). King (1887-1888) separated varieties *lambertiana, wightiana,*

forbesii, and *caulocarpa* from what his text called "*F. infectoria* Roxb., typical form," and the caption of his plate 75, "*F. infectoria* forma *typica*"; and he listed the synonyms of this form separately from those of his varieties. Domin (above) 562 added varieties *cunninghamii*, *fraseri*, and *psychotriifolia*, but did not include *typica* with the others. On p. 563, however, he spoke of *typica* with a reference to King's treatment of *F. infectoria* Roxb. in his text of (1888). Domin's other varieties, also found in Australia, had previously been combined by F. M. Bailey as *F. cunninghamii*, a synonym of *F. infectoria* Roxb. They were transferred by me to *F. lacor*. (Amer. Midl. Nat. 36: 423. 1946. [Jan. 1947.]

F. lacor var. *cunninghamii* (Miq.) M. F. Barrett has been discussed at length in the above reference. It is often seen in Florida in cultivation and is distinguished from var. *typica* by its more nearly oblong, high-shouldered leaves with an abrupt acumen, and by its endemic distribution, Australia. Its blade-veining and almost all other characters are like those of var. *typica* and leave no doubt as to its connection with *F. lacor*.

F. lacor var. *lambertiana*.—Although I saw no specimens in Florida and found no reports of this variety from that state I believe it possible that it may have been introduced in later years. Possibly it has been confused with a similar form. For these reasons a brief summary is given here.

FICUS LACOR VAR. LAMBERTIANA (Miq.) M. F. Barrett, Amer. Midl. Nat. 36: 425. 1946. Ja 1947.

Ficus sp. Wall. Cat. no. 4485 D. 1831. Under *F. populifolia* Vahl. *Nomen nudum. F. rigida* Hb. Ham. ex Wall. Cat. no. 4527. 1831. Not Jack (1822), Blume (1825), Desfontaines (1829), or Miquel (1867). *Nomen nudum. F. punctata* Hb. Heyne ex Wall. Cat. no. 4569. 1831. Not Thunberg (1786) or Lamarck (1788). *Nomen nudum. Urostigma lambertianum* Miq. Hook. Lond. Jour. Bot. 6: 565. 1847. *U. aegeirophyllum* Miq. *Ibid.* ? *U. perseaefolium* Miq. *Ibid.* 6: 567. *U. infectorium* Thwaites, Enum. Pl. Zeylaniae 265. 1864. *U. wightianum* Thwaites, *Ibid.* In part. *F. aegeirophylla* (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 216. 1867. *Nomen nudum. F. lambertiana* (Miq.) Miq. *Ibid.* 3: 286. *F. infectoria* β *aegeirophylla* (Miq.) Miq. *Ibid. F. infectoria* var. *lambertiana* (Miq.) King, Ann. Bot. Gard. Calcutta 1: 63. pl. 76. 1887-1888.

This variety often has been collected and seems well-marked, although not always well-labeled. It is distinguished from var. *typica* by its usually hairy parts, except the leaves and, occasionally, the figs. The blades typically are broad-ovate, but sometimes are broadest near the middle or are narrow-ovate. Their veining is like that of var. *typica*. They measure to 17.5 x 10 cm. (examples: 15 x 9.5, 12 x 7.5, 9 x 5.5 cm.), have a rounded, narrow, or subcordate base, a gradually narrowed and then abruptly short-acuminate apex, globose or obovoid receptacles to 17.5 mm. in greatest diameter when fresh, and 8-13 mm. when dry, with sometimes pebbly surfaces and peduncles 5-7.5 mm. long. Three forms, all more or less hairy and with pedunculate and larger receptacles than those of var. *typica*, were differentiated by Haines (1924) 831.

Type: Bombay, India. *Lambert* coll.?

Distribution: Peninsular India (less common in north than in other parts), Ceylon, Australia (Queensland). Perhaps in Java.

Additional illustrations: The illustrations of Brandis (1906) 602. pl. 186; and of Francis, Australian rain-forest trees f. 27, seem to represent this variety.

Specimens: (NYBG) *R. B. Stewart* 770, *C. T. White* 10184, *Kew Hb.* 2724 (from Wight's herbarium), and *Univ. of Mich. collections in NW. India* 4339, 4565. Wight's specimen is labeled *U. Lambertianum* Miq. The rest are entitled *F. infectoria* Roxb.

Most of the items in the above synonymy were listed by King (1887-1888). *U. infectorium* Thwaites has been included because it was described as sometimes having peduncles, and because *U. aegeirophyllum* was given as one of its synonyms. It is probable that Australian reports of *F. infectoria* made by F. M. Bailey before 1913 were really of var. *lambertiana,* since at that time he considered "*F. Cunninghamii*" an independent species. In 1913 Bailey declared that "*F. infectoria* var. *Lambertiana*" was a common Queensland form.

King's *F. infectoria* var. *wightiana* was not seen by me in Florida, nor did I find reports of it; at least under that name. In the herbarium of the New York Botanical Garden most of the specimens are from southwestern China and bear the name *F. wightiana.* They have leaves much like those of *F. lacor* var. *typica* in general shape, but tend to be more nearly oblong. The veining is entirely different. The figs are usually stalked and somewhat pebbly as to surface.

The name *F. wightiana* was given by Wallich to a specimen in Wight's herbarium which came from "Bongaloor" (Bangalore), Mysore, India, and was listed as no. 4540 in Wallich's catalog. Wallich noted that it was near *F. tsjela* Ham. (see above). Miquel (1847) 6: 566 transferred the species to *Urostigma,* but returned it to *Ficus* in (1867) 3: 286, adding *U. perseaefolium* as a synonym (see var. *lambertiana* above). In 1861 Bentham (p. 327) described a tree in Hongkong as *F. wightiana* Wall., saying that it agreed with indifferent specimens of that name from India, and citing Miquel as a reference. King (1887-1888) 1: 63 wrote down Wallich as the author of *F. wightiana* and referred also to Miquel. Later in the text, under "Errors and Omissions" he included Bentham as a reference. Later botanists acknowledged sometimes Wallich, sometimes Bentham, and occasionally both as authors. Only a few followers of King [Koorders & Valeton, Cooke, Fischer (1928) 8: 1363, and others] have accepted *wightiana* as a variety.

F. superba (Miq.) Miq. Ann. Mus. Lugd.-Bat. 2: 200. 1866. has been declared synonymous with *F. wightiana.* If so, the latter name should stand. Its principal difference from *F. superba* lies in its lack of hairiness.

A variety, *majus,* proposed for *U. wightianum* by Thwaites (1864) has been allocated to *F. mooniana* King, by King.

F. infectoria var. *forbesii* King (1887-1888) 1: 63. pl. 78. This seems at best an unimportant form, and at the worst merely a small-leaved variation of var. *typica* or var. *cunninghamii.* According to Koorders & Valeton it was named by King from a single specimen, *H. O. Forbes* 2701, collected in Sumatra. King gave the distribution as Celebes and Timor, as well as Sumatra. It has been illustrated by Koorders & Valeton (1916) pl. 745, and described briefly by H. O. Forbes (1925) 63: suppl. 108.

F. infectoria var. *caulocarpa* (Miq. 1847) King (1887-1888) 1: 65. pl. 79 was based by King upon *Urostigma caulocarpum* Miq. a Philippine species, and upon a specimen from Borneo. Specimens in the herbarium of the New York Botanical Garden show leaves of the general shape of *F. lacor*, but much larger. The figs are very small and fasciculate.

On p. 184 King cited *U. stipulosum* Miq., a Philippine species described with *U. caulocarpum* by Miquel, and *F. stipulosa* (Miq.) Miq., as synonyms of *F. infectoria* var. *caulocarpa*. *F. stipulosa* now is considered the correct name. *F. caulocarpa* as a title can not be used, because Miquel (1866) 2: 235 applied it to a very different plant, from Celebes.

A synonymy and a summary of *F. stipulosa* are given by Merrill (1923) 2: 65-66.

F. infectoria var. *geniculata* was mentioned in a discussion of *F. superba* by King (1887)-1888) 1: 59, who said that *F. superba* differed from it in its tomentose stipules and larger figs. However, King (above) 64 stated that he once thought of uniting *F. geniculata* Kurz with *F. infectoria* Roxb. but decided that it differed from the latter in its more rotund blades, longer petioles and gamophyllous flowers. He illustrated *F. geniculata* in pls. 80 and 84^{x2}.

COMPARISON OF F. LACOR WITH SOME OTHER SPECIES

Throughout this study certain comparisons have already been made. However the species *F. tsjahela* Burm. f, and *F. glabella* Blume need to be differentiated from *F. lacor*.

King (1887-1888) 1: pl. 70, 84^{x} has illustrated *F. tsjahela*. This tree has no aerial roots; and its leaves may be larger, with a sometimes cordate base and a less slender acumen. The lateral veins show a greater upper angle and are not confluent in loops near the margin. The figs are borne in groups of 2-6 on tubercles in defoliated axils, may be short-peduncled, are smaller than most of those of *F. lacor*, and show no pinkish tinge. The female flowers are said to have shorter perianth parts.

F. glabella Blume, another similar species, has been pictured by King (1887-1888) 1: pl. 60, 83 °, Koorders & Valeton (1916) pl. 746 [in which the leaf looks like F. *retusa* var. *nitida* (Thunb.) Miq.] and Senn (1913) 10^{4}: pl. 21 a. This has several varieties near *F. lacor* in appearance. The typical specimens differ from *F. lacor* var. *typica* mainly in their smaller leaves and in their figs. The leaves of one of Blume's specimens show slightly ob-elliptical leaves with a narrowed base and a very short acumen, although some varieties are more like *F. lacor*. Leaves and figs usually are smaller than those of *F. lacor*. The figs are sessile or pedunculate, purple to black, and sometimes white- or yellow-dotted. The leaves do not have the wide-meshed veining of *F. lacor*. King's pl. 83° shows ovate sepals in the flowers.

SUMMARY

The species described by Roxburgh in 1814 and 1832 as *Ficus infectoria* is not, as Roxburgh thought, *F. infectoria* Willd., which is *F. tsjahela* Burm. f.

Since the name *F. infectoria* can not be used, that of *F. lacor* Ham. which is the next in order of chronology and validity, has been substituted. It has so been acknowledged by certain botanists, for many years.

As a variable species *F. lacor* shows many forms. Koorders (in Koorders and Valeton) (1906) has said that in his herbarium almost all forms ran into each other so that differentiation was difficult. Nevertheless distinctions are seen in leaves, figs, and geographical distribution, so that wherever extremes are well-marked, varieties with the same basal characters may be considered valid.

Valid varieties are *typica*, primarily a north Indian form, but much planted in other parts of Asia and perhaps native there; *cunninghamii*, endemic in Australia; *lambertiana*, in India except (usually) in the north, and in Australia. King's other varieties have not been generally accepted. Var. *wightiana* probably is the Chinese *F. wightiana* Wall., of which *F. superba* (Miq.) Miq. is a hairy form. Var. *forbesii* probably is a small form of var. *typica*. Var. *caulocarpa* is *F. stipulosa* (Miq.) Miq., from the Philippines. Domin's three Australian varieties have been allocated to var. *cunninghamii*.

Among the suggested synonyms of *F. lacor*, *F. lucescens* Blume was invalidated by Koorders & Valeton. *F. fecundissima* and *F. pseudo-religiosa* have been repudiated by Rehder (1936). New York specimens show no affinity to *F. lacor*.

FICUS MYSORENSIS

The typical form of *Ficus mysorensis* differs somewhat in leaf and fig from its two recorded varieties, and here is designated as var. *typica*.

Ficus mysorensis var. **typica** M. F. Barrett, var. nov.

[*Katou-alou* Rheede, Hort. Mal. 3: 73. pl. 57 (*Catu-alu*). 1682]. *F. citrifolia* Willd. Sp. Pl. 4: 1137. 1806. Not Miller 1768 or Lam. 1788. *F. mysorensis* Heyne ex Roth MS. in Roem. & Schult. Syst. Veg 1: 508. 1817. *F. mysorensis* var. *pubescens* Roth in Roem. & Schult. *Ibid.* Not *F. mysorensis* var. *pubescens* (Roth, *F. pubescens* in Roem. & Schult. 1: 512. 1817) King. *F. mollis* Spreng. Syst. Veg. 3: 779. 1826. Not Vahl 1790, Willd. 1801, or Miq. 1867. *F. gonia* Ham. Trans. Linn. Soc. 15: 137. 1827. *Urostigma mysorense* (Heyne ex Roth in Roem. & Schult.) Miq. Hook. Lond. Jour. Bot. 6: 574. 1847. *F. cotoneaefolia* Alston, Suppl. Trimen. Handb. Ceylon 6: 268. 1931. Not Vahl 1806.

A tall spreading tree in its native home, to 30 ft. or more in Florida; occasionally an epiphyte; trunk short, base bearing props or buttresses and overground roots extending to 3 m. or more; branches bearing few or no aerial roots; bark light-colored, smooth at first or scaling when rubbed, becoming thick and rough; young branches almost or quite glabrous, with longitudinally elongated lenticels; twigs green to green-brown, rusty or light-hairy, about 1 cm. in diameter; terminal buds to 2.5 or 3 cm. long, 5 mm. in diameter at the base, narrowed to a sometimes hooked acuminate tip, reddish-brown, light-hairy, scales broadly triangular; leaves in 5 spiral rows, said to be red when young, leathery, drying stiff and flat; petioles 2-4 cm. long, stout, rusty- or white-hairy at first, or scaly; blades elliptic, ovate-elliptic, or obovate- elliptic, to 25 x 14 cm. in size (examples: 11.5 x 7, 16.5 x 8.5, 23 x 13 cm.); apex

rounded or slightly narrowed, then abruptly acuminate, acumen 1-2 cm. long, narrow, sharp to blunt; blade base obtuse, rounded, or subcordate; margin entire, cartilaginous; upper surface more or less hairy, becoming glabrous, finely papillose, dark green, not usually shining; under surface rusty- to ashy-hairy, becoming almost bare, papillose; midrib and other large veins yellowish, straight and prominent on under surface, midrib continuous, bearing a gland above the blade base at the intersection with the petiole; 3-4 irregular sets of basal veins, the largest set almost parallel with the lateral veins, but slightly more curved; 10-13 (usually 11) sets of lateral veins in the body of the blade, forking near the margin and uniting to form a marginal vein, upper angle at midrib near 55°; interveins showing a herring-bone pattern made by 2 or more differently sloping rows of oblong reticular spaces meeting in a zigzag line, occasionally a heavier veinlet parallel to a lateral vein; no checkered background; young receptacle said to be enclosed at first in a calyptriform covering; figs axillary, sessile, paired, ovoid or ellipsoid or slightly obovoid, to 2.5 cm. long, becoming obtuse or depressed at the apex, base rounded, red-orange and yellow-punctate, scaly or hairy to bare; a few apical bracts, not prominent; basal bracts 3, broad-triangular, blunt, leathery, spreading, at first densely covered with bristly hairs; flowers (as reported by King or Gagnepain) all in one receptacle; male flowers near apex, pedicellate, perianth of 3 or 4 almost united sepals, stamen one, anther cells subglobular; gall flowers broad, smooth, style short, subterminal; female flowers almost gamosepalous, 3-lobed, ovary ovoid, style lateral, elongated and thickened at the apex.

Type: *B. Heyne coll.* Mysore, India.

Distribution: Peninsular India, especially in south, Burma, Ceylon, French Indo-China. Introduced into the West Indies, Florida, California and elsewhere.

Economic importance: Used as a shade for coffee in south India.

Common names: Mysore Fig. East Indian Fig.

Illustrations: Rheede, King, Ann. Bot. Gard. Calcutta 1: pls. 14, 81[d]. 1887-1888.

Good descriptions additional to those in the synonymy: Cooke (1907) 2: 645-646, Gagnepain (1928) 5: 765-766, King (above) 1: 19-21 and (1888) 5: 500, Kurz (1877) 2: 440, Roth (1821) 390, Trimen (1898) 4: 86-87. Hasskarl (see footnote to *F. hispida*) has a list of synonyms and allocations. Of the Florida writers Nehrling (1944) 1: 317 reported that it was killed by frost at Sanford. Sturrock & Menninger [1946] 138 speak of it as a hardy tree of striking appearance suitable for general planting. G. R. Wilson (1938) 65 included it in a tentative list for southern Florida.

Specimens: Living trees at CF, DCN, Ed. FM (grounds of Edison Park School), FTG, MCC, MK, and in nurseries and private estates. Herbarium specimens: (NYBG) *Wight* 2646 (*U. mysorense*). *Mrs. Kanoth Yeshoda* 539 (*F. mysorensis*) from south India. Other specimens were studied at AA, BH, and US. *D. Fairchild* 3419, seen at FTG, has narrower and more rusty-hairy leaves than those usually seen in var. *typica*, but otherwise corresponds to it, and to the description in Kurz (above).

SYNONYMY

Katou-alou Rheede has been accepted by Miquel, King and others as the prototype of *F. mysorensis* on the strength of the accompanying plate. Here the leaf-shape and lateral veining and the large ovoid figs identify the species, although basal veins in the blade are lacking. The text is satisfactory in its description of these organs, but most misleading as to the tree's habit; for it

speaks of propagation by fibers as in *Itty-arealou* (*F. retusa* var. *nitida*, thus indicating a banyan habit, and it cites synonyms belonging to the ancient *F. indica*, the giant banyan described by Theophrastus and Clusius.

This synonymy, which may have been the work of Rheede's editor, Jan Commelin, was quoted by those who copied his allocations, and resulted in the placing of *Katou-alou* as the third and last synonym of *F. indica* L. in the first edition of Linnaeus's *Species Plantarum* (1753). However, the conglomeration of species which Linnaeus had assembled under *F. indica* and its variety eventually came under criticism by later botanists. Finally it became apparent that "*F. benghalensis*" (*F. bengalensis*), which Linnaeus, also in 1753, had described from his own knowledge, was the same as the ancient *F. indica* of which he had merely read. Therefore the latter name was abandoned until Miquel in 1867 illegally resurrected it for a Philippine species. *Katou-alou* was not transferred to *F. bengalensis*, which had entirely different leaves and figs and had been well illustrated by Rheede under the name *Peralu*.

The above paragraph explains why *F. indica* L. "in part" is sometimes listed as a synonym of *F. mysorensis*. Occasionally a different author is mentioned: one who followed Linnean texts. Since Vahl (1806) 2: 189 confined the title *F. indica* to the Linnean variety of that species and re-named the type, *F. cotoneaefolia*, the latter name "in part" sometimes is mentioned as a synonym. But such connections seem too slight to be included here.

F. citrifolia Willd. was the first Latin binomial which *Katou-alou* acquired and would be the valid name instead of *mysorensis* if it had not already been used by Miller and Lamarck for two other species. Willdenow said that he described the tree from Rheede's text and plate, and that it was not like *F. indica*, although sometimes it had been put under that form. *F. citrifolia* Willd. has been accepted as a synonym by Thwaites (1864) 265 and by most later writers.

F. mysorensis.—Roth, or Heyne in Roth often are mentioned as authors of *F. mysorensis*, and the source of publication usually has been cited as Roth's *Novae plantarum species* 390. 1821. In that book Roth said that *F. mysorensis* was so named by its collector, Benjamin Heyne. But part of Roth's manuscript of that book had already been quoted for *F. mysorensis* by Roemer & Schultes (1817), who thus credited the authorship to Roth, mentioning Heyne only as having seen the tree. Since that omission was rectified by Roth the authorship should read Heyne ex Roth in Roemer & Schultes.

F. mysorensis var. *pubescens*.—Roemer & Schultes and Roth declared that Heyne observed this variety in Mysore, although Roth added that the specimen came to him without specific name. It was said to have a slightly unequal blade-base, and silkier hairs on leaves and involucre than in *F. mysorensis typica*. These are such slight differences that the specimen must have represented a *forma* rather than a variety. As such it is cited here as a synonym of var. *typica*. However, the name var. *pubescens* was validly published and so would pre-date King's *F. mysorensis* var. *pubescens*, which was founded upon a different species.

F. mollis.—In 1826 Sprengel quoted part of the description of *F. mysorensis* by Roemer & Schultes and declared that species was a synonym of "*F. mollis* Willd. Vahl." This contradictory expression of an incorrect reduction is an indication of the confusion surrounding a well-known species usually called *F. tomentosa* Roxb.

This species with hairy ovate leaves and very small figs was named *F. mollis* by Vahl, Symb. Bot. 1: 82. 1790. Willdenow, Act. Acad. Berol. 91. t. 5. 1801 doubtfully reported another tree under Vahl's name; and, in fact, his report later was cited by Vahl himself for his own species. But Willdenow, a few years afterwards, discovered that *his* tree was not *mollis*, but a different species, which eventually became known as *F. oppositifolia* Roxb. and *F. hispida* L.f. Thereupon Willdenow (1806) 4: 1136 changed the title of Vahl's species to *F. tomentosa* Roxb., using unpublished notes by Roxburgh on a tree which evidently was the same as Vahl's. Of course *F. mollis* Vahl should replace *F. tomentosa* Roxb. for this species, as King (Ann.) 1: 22 and Alston (1931) 6: 268 have recognized.

F. gonia Hamilt.—Hamilton, writing on *Katou-alou*, believed that was the same as *F. citrifolia* Willd., and said that his *F. gonia* was very like both except for its lack of aerial roots (a mistake due to Rheede's faulty text). Miquel (1847) included *F. gonia* as a synonym of his *Urostigma mysorense*, and King found that sections A, B and C of Wallich's catalog (1831) no. 4496 were *F. gonia* from Hamilton's herbarium and were specimens of the typical form of *F. mysorensis*.

U. mysorense, of course, is a transfer of *F. mysorensis*, although Miquel may have included a synonym of one of the varieties.

F. cotoneaefolia Alston indicates Alston's belief that Vahl's should be the name of this species (see above).

Ficus mysorensis var. **dasycarpa** (Miq.) M. F. Barrett, comb. nov.

Ficus pubescens Roth in Roem. & Schult. Syst. Veg. 1: 512. 1817. *F. tomentosa* Hb. Madras ex Wall. Cat. no. 4499. 1831. Not Roxb. *Nomen nudum. Urostigma dasycarpum* Miq. Hook. Lond. Jour. Bot. 6: 574. pl. 23 B. 1847. *F. mysorensis* var. *pubescens* (Roth in Roem. & Schult. *F. pubescens*) King, Ann. Bot. Gard. Calcutta 1: 20. 1887-1888. Not *F. mysorensis* var. *pubescens* Roth.

This variety (which I have not seen) is more densely hairy than var. *typica*, with a longer, more copious, and deep rusty-red tomentum, according to Cooke (1907) 2: 646, on twigs, leaves (both surfaces at least at first), and receptacles. According to Miquel (above) the petioles measure 0.5-1.5 cm., and the blades 8-10 x 5-7 cm. The latter are broad-ovate and have 8-10 sets of lateral veins and an obtuse or short-acuminate apex. Receptacles and other leaf characters appear to resemble those of var. *typica*.

Type: Benjamin Heyne coll. "India Orientalis."
Distribution: Madras?, Bombay, Ceylon.

Roth described *F. pubescens* at length, but without measurements, in his MS used by Roemer & Schultes and in his own text (1821) 1: 387. In so

doing he differentiated it from his *F. mysorensis* var. *pubescens*, in which he could find few characters not belonging to what here is called var. *typica*. He said that the type specimen of *F. pubescens* came to him unnamed from Heyne.

Miquel (1847) 6: 573 declared *F. pubescens* Roth a synonym of *U. tomentosum* (*F. tomentosa* Roxb.). The latter species, whose correct name is *F. mollis* Vahl, has been described with many of the same characters as *F. pubescens*, but also with pea-like figs instead of the cherry-size mentioned by Roth. King has stated that *F. pubescens* fits *F. mysorensis* better than *F. tomentosa*. However, he identified Wallich's *F. tomentosa* as variety *pubescens* of *F. mysorensis*.

Miquel (1847) 6: 574 described *U. dasycarpum*, from Bombay and Ceylon. Although some of Roth's characters of *F. pubescens* seem contradicted in this account the discrepancies may be only those due to different size and age of the tree or to another interpretation of the terms used. In (1867) 3: 285 he called *U. dasycarpum* "forma *parvifolia*" of *F. mysorensis*.

King made it plain that his own var. *pubescens* was based upon Roth's species described on p. 387 of the 1821 text; but he paid no attention to the fact that the variety had been published in the same book and in Roemer & Schultes' work, with application to a different form. Under modern rules that name can not be used again. Therefore Miquel's specific name for his *Urostigma* species has been substituted.

An additional synonym, *F. rupestris* Ham. was suggested by King. But Hamilton's description includes rooting fibers from branches, cordate leaves, and pea-like figs. He himself differentiated *F. rupestris* from *F. mollis* Vahl only because Vahl had listed solitary figs, while those of *F. rupestris* were paired. But the number of figs at a node is apt to vary with the stage of maturity, another reason given by King seems illogical, and Miquel has declared that from Hamilton's description *F. rupestris* should not be joined to *F. mysorensis*. Most other writers on *F. mollis* (*F. tomentosa*) report paired figs.

FICUS MYSORENSIS var. SUBREPANDA (Wall.) King, Ann. Bot. Gard. Calcutta 1: 20. pl. 15. 1887-1888.

Ficus sub-repanda Wall. Cat. no. 4568 A. 1831. *Nomen nudum*. *F. lateritia* Wall. *Ibid.* no. 4496 D. Under *F. mysorensis*. Specific name *lateritia* not in text. As synonym. *F. hookeri* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 215. 1867. Not Sweet 1826. ? *F. stupenda* Miq. *Ibid.* 3: 286.

Type: Wallich coll.? Name of place illegible.

Distribution: Not in S. India. Replaces other forms in the eastern base of the Himalayas, Khasi Hills, Burma, 1000-2000 ft. (King's statements.) See also below.

Specimens: (CF) One tree of var. *subrepanda*, *P.I.* 47833 from plants from Darjeeling, India. One tree labeled *F. hookeri*, from seeds from Darjeeling, India, *P.I.* 80082. Also herbarium specimens from these trees, *Fennell* 1560 and *Fennell* 1523, seen at BH. My own specimens from them were collected in 1938 and 1949. At NYBG *Hb. Mus. Paris* 2198, *Poilane coll.*, from Laos, seems to be this variety.

King based this variety upon Wallich's specimens. The name *lateritia* may

have come from a labeled specimen of 4496 D. King described the leaves as larger than those of the typical *F. mysorensis*, glabrous when full grown, subscabrid and dotted, often narrowed, with 7-9 basal veins and 12-20 sets of lateral veins. The figs were ovoid to globose, about 4 cm. across, orange-red and smooth. His plate shows a leaf 25 x 14 cm., with a petiole 6 cm. long. A fig is 5 x 4.5 cm. in size and bears warts or pustules. The hairy terminal bud is 3.5 cm. long and 8 mm. across at the base. Other characters are like those of var. *typica*.

As seen at Chapman Field the specimens of *F. subrepanda* and *F. hookeri* seemed to be the same species or variety. The trees were about 12 m. tall, with short trunks and buttresses, and overground roots extending 3 m. from the trunk. The crown was about 12 m. in diameter. The twigs retained hair until the end of the first year. Their greenish-brown bark became gray at the age of two or three years, but kept its smooth, sometimes shredding, surface and yellowish, elongated longitudinally lenticels until the branches became old. Some blades were no larger than those of var. *typica*, but others measured up to 32 x 19 and 33 x 14 cm. The figs measured 4.5 x 3 cm. or more when mature, and with their bright red color and ovoid shape looked like large strawberries. They bore warts of the same color. Other characters were like those of King's description or of the typical form. Miquel's description of *F. hookeri* and King's plate 42 of that species show immature figs partly enveloped by an involucre of basal bracts.

Valeton (Icones Bogoriensis 3: 91-92. pl. 237. 1908) described and illustrated *F. stupenda* Miq. He said that there had been only one specimen of it, Zollinger's in Hb. Utrecht, but that Koorders had found it in west Java and in the Buitenzorg Garden. He remarked that it seems near *F. mysorensis*, which Valeton had not seen, and then characterized and pictured large, hairy leaves and receptacles like those of var. *subrepanda* except for rather fewer large veins and transverse veinlets (although he said the latter were not conspicuous). Although *F. stupenda* is an excellent likeness of *F. mysorensis* var. *subrepanda*, King had believed that it was the same as *Urostigma giganteum* Miq. (1854) 90, 96; although Miquel (1859) 12: 351 had said that *U. giganteum* had leaves only 5-9 x 2 cm. in size.

SUMMARY OF F. MYSORENSIS

The specific name *mysorensis* indicates truthfully that this is a form of southern India, although at least one variety, *subrepanda*, is native to a cooler climate. This and var. *typica* have been introduced into south Florida.

The species is characterized by hairy twigs, buds, leaves, and receptacles; and by stiff, straight- and heavily-veined, almost elliptic leaves with several sets of basal veins and rather few lateral veins for the size of the blade. These are connected by a herring-bone pattern of veinlets. The figs are large, ovoid, red-orange, and sometimes with concolorous warts. There are no secondary trunks from aerial roots, although epiphytic roots may unite to form the surface of the trunk and may continue as buttresses and overground roots.

Var. *typica* has medium sized organs as compared with the other varieties, and less permanent hairiness. Its progenitor is Rheede's *Katou-alou*, which Linnaeus incorrectly associated with his *F. indica*, now known as *F. bengalensis*. Numerous other synonyms have been collected, mostly by King.

Var. *dasycarpa* is a substitute name for King's var. *pubescens*, which is nonvalid because Roth previously had used that combination for a form almost exactly like the typical *F. mysorensis*. Var. *dasycarpa*, like var. *typica*, is a southern form, but differs in greater hairiness and smaller organs.

Var. *subrepanda* replaces the other varieties in north India and some Himalayan states, and in high altitudes in other countries. It has larger and more nearly glabrous organs than the other forms. It seems to be the same as *F. hookeri* Miq. and *F. stupenda* Miq.

The date of publication for *F. mysorensis* should be 1817 instead of the usually held 1821.

FICUS RELIGIOSA L.

Ficus religiosa is easily recognized by its attractive and unique leaves. The blade is somewhat triangular, ends in a long lash-like tip, and trembles in a breeze because of its long flexible petiole.

This Indian species always is found near Buddhist temples, for it is the holiest tree of that cult. It is said to have appeared first when Gautama was born, and it was under it that Gautama meditated for six years while he was receiving complete knowledge as to the meaning of existence. This is called his incarnation as Buddha, and is assumed to have occurred in Gaya, northern India, about 520 B.C. The leaves still tremble when they remember those meditations.

For these reasons common popular names for the species are Bo Tree (*bo* being the Sanscrit word for knowledge) and *Bodhi*. *Buddha* comes from a word related to *bodhi*. Hindus, also, hold the Bo Tree sacred, believing that Vishnu was born under one.

The abundance of *F. religiosa* in Ceylon dates from the third century B.C., when Buddhist missionaries were sent there from India. The converts begged the contemporary Indian monarch for a cutting of the original tree. This request, although willingly granted, involved the problem of obtaining the cutting without violating a rule that no part of the sacred tree should be severed. However, a vermilion line was made around a twig, and in a miraculous manner the slip dropped off, complete with roots, into a golden vase filled with scented soil. This was conveyed with much ceremony to Anuradhpura, about 80 miles north of Kandy in Ceylon, and there planted and provided with suitable buildings for worship and for its attendants. Tennent (Ceylon 1: 341-343, and 2: 613-619, 632-636. 1860) has discussed this tree in detail, has called it the oldest historical tree, and has quoted from its written history, which then had been kept for about 2000 years. It also has been spoken of as a living antiquity.

The following synonymy has been extended to cover early names in Latin

form, which furnish a picturesque background for the more modern nomenclature.

FICUS RELIGIOSA Linnaeus, Sp. Pl. ed. 1: 1059. 1753.

[*Arealu* Rheede, Hort. Mal. 1: 47. pl. 27. 1678]. [*Arbor diaboli* Rheede, *Ibid.* 1: 48]. [*Ficus malabarensis folio cuspidato, fructu rotundo, parvo, gemino* Syen *in* Rheede, *Ibid.* 1: 48]. [*Arbor daemonum belgis* Hermann, Mus. Zeyl. 42. 1717]. [*Arbor zeylanica, religiosa, foliis perpetuo mobilibus* J. Burm. Thes. Zeyl. 29. 1737]. [*Ficus foliis cordatis integerrimis acuminatis* L. Hort. Cliff. 471. 1737]. [*Pimpal, sive pipal indiae orientalis* Zanoni, Rar. Stirp. Hist. 179. 1742]. [*Pimpal arbore indiano* Zanoni, *Ibid.* pl. 136. 1742]. *Pippali* Jones, Asiat. Res. 4: 309. 1795. *F. caudata* Stokes, Bot. Mat. Med. 4: 358. 1812. Not Wallich or Griffith. *F. superstitiosa* Link, Enum. Hort. Berol. 2: 449. 1822. *F. religiosa* var. *rhynchophylla* Wall. Cat. no. 4487 E. 1831. *Nomen nudum. F. rhynchophylla* (Wall.) Steud. Nom. Bot. ed. 2, 1: 637. 1840. *Urostigma religiosum* (L.) Gasp. Nov. Gen. Fici 7. 1844. *U. affine* Miq. Hook. Lond. Jour. Bot. 6: 564. 1847. ? *F. peepul* Griff. Notul. Pl. 4: 393. 1854. *F. religiosa* β *cordata* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 287. 1867. In part.

Epiphytic or separate tree, medium-sized to large, almost entirely glabrous; crown spreading, densely leaved; trunk often pitted, ribbed, or appearing composed of several small trunks if made by dangling epiphytic roots which have covered the trunk of a supporting plant; bark of the trunk of an independent tree smooth at first, reddish-brown or light-colored, exfoliating in irregular scales when old; base of trunk often buttressed and surrounded by a network of roots spreading over the ground and sometimes invading masonry; lowest branches near the ground in an independent tree, almost or quite rootless, surface like that of a young trunk; twigs tan-colored, becoming glabrous, lenticellate and showing encircling stipule scars; terminal buds green or tan, conical, about 1 cm. long and 4 mm. thick when quiescent, their stipules ovate, acute, glabrate, deciduous; leaves in 5 spiral rows, sometimes deciduous; petioles 5-10-14 cm. long, slender, glabrous; blades deltoid or broad-ovate; reported to 28 x 16.5 cm., usually smaller (examples: body of blade 11.5 x 11 cm., tip 5.5 cm., petiole 9 cm.; body 8.5, tip 5, petiole 11.5 cm.); apex gradually narrowed, then abruptly forming a slender cusp a few mm. wide at the base and narrowed to an acute tip reported to 9 cm. long; base of blade usually truncate and rounded at ends, occasionally subcordate, rarely a little decurrent; texture thin, but stiff when dry; margin slightly undulate; upper surface shining, light- to dark-green, sometimes reddish along veins, punctate and sometimes pellucid punctate; under surface dull, sometimes lighter in color than the upper surface, minutely tuberculate when dry; veining distinct; midrib lighter in color than surface of blade, continuous to apex of cusp; one or more pairs of basal veins, differing only in angle from the 8-10 sets of lateral veins; lateral veins forking and uniting to form a deeply indented submarginal vein; no continuous transverse veins from adjacent laterals; largest reticular spaces forming a usually 2-rowed herring-bone pattern in the interveins; figs axillary, paired, sessile, globose or depressed-globose, usually 1-1.5 cm. in diameter, smooth, dark purple or black; ostiole closed by 3 apical bracts, raised at first, then depressed; basal bracts 3, about 5 mm. in diameter, broad, sometimes notched at the apex, slightly hairy; male flowers said to be sessile, 3 perianth parts, one stamen with a short filament; female and gall flowers sessile or short-pedicelled, 5 peri-

anth parts, style short and lateral, stigma cylindrical or rounded, ovary ovoid; gall flowers often without a perianth; male, female, and gall flowers in the same receptacle.

Type: "India."

Distribution: Native to the sub- Himalayan forest from the Punjab eastward, including Bengal, Orissa, the Circars, and central India; elsewhere frequently cultivated or naturalized [See Duthie (1915) 31: 151]. Now found in many countries in tropical or sub-tropical climates. Planted in southern California as well as in Florida, and in Honolulu.

Economic importance: Elephant fodder, food for silk "worms," lac, rubber, tanning materials, bird lime, medicine, mouth wash, box material, firewood, charcoal. Masonry sometimes injured by the growing roots. Buddhists and usually Hindus refrain from cutting this species, but Mohammedans have no such inhibition.

Specimens of living trees were seen at CF, DCN, FM (on High School grounds), FTG, KW, MCC, MK, and many places in Miami, such as Bird Ave. Herbarium sheets were examined at all the herbaria. They included specimens from Bay Front Park, Miami, and from Boca Grande (Fla.); also from Montecito and Santa Barbara (Calif.).

References additional to those in the synonymy.—Most books on Indian botany, such as those included in the following text, contain descriptions of *F. religiosa*. Additional illustrations may be seen in Beddome (1874) 2: pl. 314, Koorders & Valeton (1916) pl. 743, King (1887-1888) 1: pl. 67 A, 84[II], Miquel (1859) pl. 23 D, Mowry (1938) pl. 43, Tennent (above) 1: pl. p. 614, Wight (1853) 6: pl. 1967.

The value of *F. religiosa* as a street and lawn tree is attested by Mowry (1938) 52, 54-55; Nehrling (1944) 1: 117-119, 338-339; Royal Palm Nurseries (1938) 15; Simpson (1926) 153; and Sturrock & Menninger (1946) 140.

SYNONYMS OF FICUS RELIGIOSA

In Hortus Indicus Malabaricus.—Rheede's description and plate of *Areal'u* are very good and have been much cited. *Arealu* is the transliteration of the name in Arabic characters which appears on the plate. The second part, *-alu*, signifies a fig. The text speaks of the name *Arbor diaboli* as given to Vishnu's sacred tree by Christians, and also adds the "Brahman" name *Bipaloè*, which obviously is a form of *Pipal*, a common vernacular title in India. An unsigned note at the end of the text states that a suitable name is the polynomial which may be translated into English as Fig of Malabar, with a pointed leaf and round, small, paired fruit. This polynomial was the work of Arnold Syen, who wrote the notes and commentaries for Rheede's first volume, in spite of the statement on the title page that the editor was J. Commelin. The remaining volumes of the work were edited by Commelin. [See K. Commelin (1696) 28.]

Synonyms from Ceylon.—These are contained in books by Paul Hermann, J. Burman, and Linnaeus. I have not seen Hermann's work, which ran two editions, and find Burman's references to it confusing. Burman followed his own polynomial immediately with the words: "Arbor Daemonum Belgis Mus. Zeyl. pag. 42." Then he cited native names: *Boghas, Budughas*, etc., and a note that the Singhalese venerate this tree because Buddha instructed them under it. Immediately after this note he again gave the source "Mus. Zeyl." Although Linnaeus and others have cited only the native names as coming

from Hermann I have inferred from the above that he was responsible also for the Latin phrase.

The text by Linnaeus will be mentioned later.

Zanoni's names.—Zanoni's plate of the Indian tree *Pimpal* certainly represents *F. religiosa,* as is shown by the very long narrow cusp and the numerous parallel lateral veins. His text cites the alternate name *Pipal* and refers to *Arealu.* I have seen no reference to Zanoni except by Lamarck (1788) 2: 493.

Linnean references.—Linnaeus came to the University of Leiden in 1735 and apparently there found an "angel" in the person of Herman Boerhaave, who in 1753 had resigned his directorship of the botanical garden of the Leiden-Batavia Academy, but was continuing his interest in botany by aiding researches and publications. Hunger (1918) 23: 356-357 has said that Boerhaave assisted Linnaeus, and probably helped to turn his attention from medicine to botany. He recommended Linnaeus to describe the plants in the collections of George Clifford of Leiden and to collaborate with J. Burman in the latter's *Thesaurus Zeylanicus.* Although this book and the study by Linnaeus of Clifford's garden came out in the same year, 1737, there is no evidence, so far as the Bo Tree is concerned, that the two authors worked together. The name given by Linnaeus to Clifford's specimen of this tree described the untoothed blades with their heart-shaped base and sharp-pointed tip, while Burman emphasized the fluttering leaves of the sacred tree of Ceylon. Linnaeus, but not Burman, cited *Arealu* as the prototype of his species. However, in Linnaeus's own flora of Ceylon (1747) 177 and (1748) 177-178 the author, although retaining his own polynomial for the Bo Tree, referred to Burman's title, as well as to Hermann's vernacular names.

Linnaeus may have derived the specific name *religiosa,* in *Species plantarum,* from Burman, whom he did not mention there. His citations were of his earlier books, of Rheede, and of an illustration made by Plukenet (1692).

The reference to Plukenet needs a little explanation, since it has been made by many writers and usually has been accompanied by Syen's polynomial, attributed to Plukenet. But Plukenet, whose pl. 178, f. 2 appears to be a good representation of the typical leaf of *F. religiosa,* labeled it *Ficus malabarensis folio cuspidato, fructu rotundo, parvo, gemino* Syen, and referred to Rheede and to the Singhalese name *Bogah.* Miller, who introduced *F. religiosa* into England in 1731, in early editions of his *Gardener's dictionary* described the tree under Syen's name and authorship and said that the seeds came from Jamaica. He referred to Plukenet (1696) 144-145. Plukenet's illustration had been placed on the same sheet with three West Indian species. In later editions Miller's work called the tree by Linnean names, substituted Plukenet's name for Syen, and listed India as the origin of the species. Linnaeus, in omitting Syen, may merely have followed the example of Boerhaave (1710) 278 and (1720) 2: 258.

Pippala.—Jones evidently considered this the Latin equivalent of the Hindu word *Pipal,* which he cited as a common name. Part of the description of this "select Indian plant," to quote from the title of his paper, is worth repeat-

ing here for its graphic English: "leaves hearted, scalloped, glossy, daggered." He spoke also of the trembling of the leaves, and described the figs correctly, if scantily. "Pippula," with a reference to Jones' study, was cited as a synonym of *F. religiosa* by Roxburgh (1832) 3: 547.

Ficus caudata.—Stokes saw a specimen of *F. religiosa* in "Fothergill's garden," and re-named it, citing Linnaeus (1763) 1514, most of the references there, and also a few more recent ones.

F. superstitiosa Link.—Link differentiated a specimen in the Royal Botanical Garden of Berlin from *F. religiosa* because of its narrowed blade-base, but Kunth (1846) 15 and (1847) III, 7: 236, writing of the same garden, cited *F. superstitiosa* Link as a synonym of *L. religiosa.* Miquel (1847) 6: 563 and (1859) 1^2: 333 approved this synonymy, but omitted *F. superstitiosa* in (1867) 3: 287.

Specimens mentioned by Wallich.—Var. *rhynchophylla* Wall., from Nepal, is division E under no. 4487, *F. religiosa,* in Wallich's catalog. Steudel (1840) 1: 637 listed this variety, but also printed *F. rhynchophylla* Wall. as a synonym of *F. religiosa.* King (Ann.) 1: 55 and (1888) 5: 513 considered that all five parts of no. 4487 belonged to *F. religiosa.* No other new name was involved. King (Ann.) 1: 183 cited *F. rhynchophylla* Wall. as a synonym. The specific name means snout-leaved.

Urostigma spp.—*Urostigma* now is only a subgenus of *Ficus.* Gasparrini illustrated his combination *U. religiosum* in (1845) pl. 7, f. 1-5.

U. affine.—Specimens from Assam and Bengal were described by Miquel under this name, but in terms that agreed with *F. religiosa.* He declared also that Wallich's nos. 4487 D and E seemed to be young specimens of *U. affine.* In (1867) 3: 287 he listed *affine* as a synonym of *F. religiosa* γ *rhynchophylla* and made 4487 D β *cordata* of *F. religiosa.* Haines (1924) 5: 834 has thought that D is partly *F. rumphii* Blume. King and Gagnepain (1928) 5: 767, both of whom have recognized no varieties of *F. religiosa,* have cited *U. affine* as a synonym of the species itself.

Griffith's species.—Griffith in 1854 published three names to designate species which resembled *F. religiosa,* a tree which he did not mention. Of these species *F. peepul* from Assam seems closest to *F. religiosa,* both in its name and in its description, although some characters might apply better to *F. rumphii.* However, that species usually is not epiphytic, as *F. peepul* apparently was. No illustration accompanied the text.

The text on *F. affinior* Notul 4: 392. 1854 is confusing. It begins by saying that this species in growth and habit is like *F. affinis* Griff. Ic. Pl. Asiat. pl. 553. 1854. Then it makes a description which ends with the remark that it refers to *F. affinis,* but which does not conform to that plate. In fact the plate, except for the larger size of the bud and the shorter apex of the blade, is closer to the characterization of *F. peepul.* The description goes on to state the similarity of *F. affinior* to *F. peepul* in its sculptured trunk and network

of roots, although it differs in the shape of the leaves and the "want of a tail." From *F. affinis* it differs in the shape of its leaves and the "sudden cuspis." But in the description of *F. peepul* and the plate of *F. affinis* the blades are deltoid, and the plate has a sudden, although short cusp.

F. affinior has been listed as a doubtful synonym of *F. religiosa* by King. On p. 55 in (1887-1888) he said that the venation of the plate differed from that of *F. religiosa*, but was not like that of *F. rumphii;* but on p. 62 he declared that Griffith's specimen of *F. affinior* in the Calcutta Herbarium was *F. infectoria* Roxb. (*F. lacor* Hamilton). *F. affinior* has been accepted for *F. religiosa* by most of those writers who followed King. Brandis (1874) 416 thought that *F. affinis* might be a species which now is considered a synonym of *F. rumphii.* Perhaps *F. affinior* belongs there, too.

REJECTED REPORTS

Arbor conciliorum Rumph. Herb. Amboinense 3: 142-145. pl. 91, 92. 1743. The text gives as synonym the names proposed by Rheede, Syen, and Linnaeus (1737) for the tree whose future binomial was to be *F. religiosa.* A native name is stated to be *Caju bodi.* One plate shows a sculptured trunk like that of old specimens of epiphytic *F. religiosa;* the other pictures an ovate leaf with an acuminate, but not dagger-like apex, and an acuminate bud. The leaf is almost exactly like one shown in a plate of *F. cordifolia* Roxb., in Wight (1843) 2: pl. 640. This species is accepted as a synonym of *F. rumphii* Blume.

Linnaeus (1759) 4: 124, in an article under the stated authorship of Olaf Stickman, approved *Arbor conciliorum* as a synonym of *F. religiosa.* However, the second edition of *Species plantarum* merely suggested a comparison between the two, and Stokes (1812) 4: 359 declared that they were not the same.

Until 1825 several other writers alluded to *Arbor conciliorum* in connection with *F. religiosa.* For instance, Lamarck (1788) 2: 493 made *Arbor conciliorum s. caju bodi* a variety of *F. religiosa.* But Hamilton (1822) 13: 488 distinguished between the two species.

In 1825 Blume established *F. rumphii,* from Batavia referring to both names mentioned by Rumphius. Nevertheless, *Arbor conciliorum* continued to be linked to *F. religiosa* by some writers until past the middle of the 19th century. More recently Merrill (N 1917) 195 has reaffirmed its identity with *F. rumphii.* Gagnepain (1928) 5: 768 has cited variations of *Caju bodi.*

F. religiosa incorrectly reported.—*F. religiosa in Forskål Flora Aegyptiaco-arabica* 180. 1775, is *F. populifolia* Vahl, according to Vahl (1806) 2: 181, King (Ann.) 1: 56 and others. That of *G. Forster, Florulae insularum Australium prodromus* 76. 1786, from an island in the New Hebrides, has been declared probably not *F. religiosa* L. by Seemann, *Flora Vitiensis* 247. 1868. The following reports belong to *F. rumphii* Blume, according to the writers named: that of Loureiro (1790) 2: 664, according to Merrill (Je 1935) 24[2]:

138; that of Wallich (1831) no. 4484 F, according to King (Ann.) 1: 54; that of Decaisne (1834), according to Miquel (1859) 1[2]: 333 and (1867) 3: 287; *F. religiosa β cordata* (Wall.) Miq. (1867) 3: 287, based on Wallich (1831) no. 4487 D, according to Haines (1924) 5: 834, but not according to King. Gagnepain (1928) 5: 767 believed that Loureiro's *F. religiosa* was valid.

Rafinesque's subgenus Spherosuke.—Rafinesque (1838) 57-58 attempted to allocate *F. religiosa* to this subgenus of his; but *Spherosuke* has not endured.

FICUS RUMPHII Blume, Bijdr. 437. 1825.

(The following material is added in order to distinguish between *F. religiosa* and *F. rumphii.*)

[*Arbor conciliorum* Rumph. Herb. Amboin. 3: 142. pls. 91, 92. 1743]. *F. benjamina* Houtt. ed. L. Pflanzensyst. 2: 539. 1777. In part. *F. religiosa* var *β Arbor conciliorum s. caju bodi* Lam. Enc. Meth. 2: 493. 1788. *F. religiosa* Lour. Fl. Coch. Chin. ed. 1, 2: 664. 1790. *F. cordifolia* Roxb. Hort. Beng. 66. 1814. *Nomen nudum. F. conciliorum* Hb. Ham. ex Wall. Cat. no. 4484 A. 1831. Under *F. rumphii* Blume *F. cordifolia* Hb. Roxb. ex Wall. Cat. no. 4484 B. 1831. Under *F. rumphii* Blume. *F. religiosa* Hb. Rupel ex Wall. Cat. no. 4484 F. 1831. Under *F. rumphii* Blume. — Hb. Ham. ex Wall. Cat. no. 4485 B. 1831. Under *F. populifolia* Vahl. — Hb. C ex Wall. Cat. no. 4487 D. 1831. In part. Under *F. religiosa. F. cordifolia* Roxb. Fl. Ind. ed. 2, 3: 548. 1832. *Urostigma cordifolium* (Roxb.) Miq. Hook. Lond. Jour. Bot. 6: 564. 1847. *F. sp.* Griff. Itin. Notes 111, no. 145. 1848. Ic. Pl. pl. 549. 1854. ? *F. affinis* Griff. Ic. Pl. pl. 553. 1854. Not Blume or Wallich. ? *F. affinior* Griff. Notul. 4: 392. 1854. *U. rumphii* (Blume) Miq. Zoll. Syst. Verz. 90. 1854. *F. religiosa* Decne. Hb. Mus. Paris ex Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 287. 1867. *F. religiosa β cordata* (Wall.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 287. 1867. In part.

Deciduous tree, not usually epiphytic; bark light-colored, smooth; trunk usually not pitted, sometimes hairy at first; terminal bud ovoid-acuminate, 1.5-2 cm. long; petioles 5-9 cm. long, stouter and stiffer than those of *F. religiosa;* blades 7.5-15 x 6-11 cm. (example: 13 x 8 cm.), broad-ovate; apex gradually narrowed to a triangular cusp 1-3 cm. long (1/6 to 1/5 the length of the blade); base truncate or decurrent on the petiole, rarely subcordate; surface of blade punctate; one or two sets of basal veins; 3-6 sets of laterals; parallelism of laterals and reticular rows not marked as in *F. religiosa;* no herring-bone effect; figs obovoid or globose, not vertically depressed, sessile, 1.5-2 cm. in diameter, glabrous, warty, pale with dark spots, becoming almost black; basal bracts 3-4 mm. in diameter, almost round, not forming a cup; perianth parts 3 in all flowers, male sepals spatulate, anther equalling filament; female flowers more or less pedicelled, sepals oval, rosy, style long, stigma clavate, ovary obovoid.

Type: Near Batavia, Java.

Distribution: Outer Himalayan ranges from the Chenab east to Assam, central and western India, Burma, Malaysia.

F. cordifolia in Graham (1839) 192, and *cordifolium* (no genus) in Dalzell & Gibson *Bombay flora* 242. 1861 have been said to be *F. arnottiana* (Miq.) Miq.

SUMMARY

The sacred Bo-tree has been known for centuries, even before the Christian era. Its very long slender leaf-acumen separates it from all others, even the somewhat similar *F. rumphii*. It has acquired many synonyms, but no varieties which are recognized at the present time.

FICUS ROXBURGHII Wall. Cat. no. 4508. 1831.

F. macrophylla Roxb. & Buch. MSS. ex J. E. Smith, Rees, Cyc. 142: *Ficus* no. 32. 1810. Not Desfontaines ex Persoon. *Covellia macrophylla* (Roxb. & Hamilt.) Miq. Hook. Lond. Jour. Bot. 7: 465. 1848. *F. sclerocarpa* Griff. Notul. 4: 397. 1854. *F. sclerocorpa* Griff. Ic. Pl. Asiaticarum pl. 558. 1854. *F. regia* Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 230. 1867. In part. Not Kurz. ? *F. macrocarpa* Lév. & Van. Mem. Acad. Cien. Barcelona III, 6: 152. 1907. *Fide* Rehder. *F. auriculata* Merrill & Chun, Sunyatsenia 2: 216. F 1935.

Usually low spreading tree or large shrub, but said to reach 10.5 m. in height; trunk short, thick, dividing into stout branches; bark gray or tan at first, sometimes rather warty; crown broad; twigs at first pale green, white-hairy; terminal buds 2-5 cm. long, conical, covered with brown or reddish, ovate-lanceolate, acuminate, velvety scales; petioles to 21 cm. long, stout, reddish, hairy at first; blades thin-leathery, broad-ovate to heart-shaped or almost round, rarely somewhat lobed, to 45 x 30 cm. or more (examples: 38 x 30, 27 x 27 cm.); apex rounded or slightly narrowed, then abruptly pointed or short-acuminate; base rounded or cordate; margin entire, wavy, or irregularly coarsely toothed; upper surface becoming bare, lustrous deep green when fresh, dull and showing whitish spots when dry; under surface hoary or gray-hairy, especially on veins; midrib very stout, continuous to the apex of the blade; basal veins 3 sets in large leaves, less in small leaves, branched on lower edge; 4-6 sets of lateral veins leaving the midrib at an upper angle of about 45° (parallel with the largest basal pair), curving toward the apex near the margin and connected at a right angle by almost straight transverse veins; similar transverse veins making loops between the midrib and the laterals and the largest basal pair; no intramarginal vein; background reticulate; figs clustered on short leafless twigs or on tubercles from root-like branches on the ground, also from the base of the trunk, and at the base of the largest branches; top- or pear-shaped or almost globose; to 7 x 8 cm. or more (receptacles containing male and gall flowers), or to 5.75 x 7 cm. (receptacles holding female flowers); pubescent at first, becoming almost glabrous; bearing 8-12 vertical ridges; green to reddish-yellow (male and gall), or green and woody to brown or purple, often with yellow or brown blotches, and soft (female); apex depressed, ostiole large, closed with numerous apical bracts which may be flat or erect; base narrowed, sometimes forming a stipe between which and the peduncle are located three deltoid, acuminate, basal bracts 5 mm. or more in length; lateral bracts rarely present on the sides of the receptacle; peduncle 3.5-4 or rarely 5 cm. long, velvety; figs in native home appearing and ripening throughout the year, said to diffuse a strong scent of Russia leather when ripe; flowers (according to King): male flowers sessile, perianth of three broad, imbricate, hyaline, inflated sepals, stamens 1-3, usually 2, anthers ovate, filament long, thick; gall flowers pedicelled, perianth 3-parted above, partly

covering the smooth ovoid ovary, style short, subterminal, stigma dilated; female flowers usually on a separate tree, subsessile or pedicelled, perianth like gall flowers, style long, curved, stigma cylindrical, achene viscid, minutely tuberculate. The female flowers may be stimulated mechanically, as by a stick inserted through the ostiole, in order to induce fertilization.

Type: "East Indies."

Distribution: Northern India and related states, Burmese Hills, Indo-China, southwestern China, Hainan. Cultivated in many other tropical and sub-tropical places.

Common name: Roxburgh's Fig.

Economic importance: The figs are eaten raw or in curries, the leaves furnish fodder for camels and elephants, the bark provides coarse fiber for ropes, the wood is heavy and hard.

Additional descriptions and illustrations: Dr. David Fairchild (Roxburghii's giant fig in Teneriffe, Jour. Hered. 18: 533-536. pls. 4-6. 1927) has given an interesting and well-illustrated account of this species. D. D. Cunningham in the appendix (13-47, pls. 1-5) and in the frontispiece to King (1887-1888) vol. 1: has discussed and illustrated the development of the embryo in female flowers and has stated that fertilization, even when brought about by insects, is induced by mechanical means and not by pollination. Other references are: Brandis (1874) 422, (1906) 609; Gagnepain (1928) 5: 806-807; Haines (1924) 5: 839; King (above) 1: 168-169. pl. 211; King (1888) 5: 534-535; Kurz (1877) 2: 460; Roxburgh (1832) 3: 556-557; Wight (1843) pl. 673. Simpson (1926) 154 mentions it from Florida.

Specimens of living shrubs were seen at Chapman Field in 1937, 1938, and 1949. Herbarium material from there (*U.S.P.I.* nos. 77952, 86675, and probably 133194) and from India and China has been examined at BH, and NYBG. Good examples from China are *R. C. Ching* 6422 from Kwangsi Province, *Y. Tsiang* 7254 from Kweichow, *F. C. How*, 70412, and *N. K. Chun & C. L Tso* 43974 from Hainan. Of other specimens some may not belong to this species. Most of the Chinese forms were labeled *F. auriculata* Lour. (see later). *A. Henry* 1310 from Formosa, a specimen cited as *F. roxburghii* by Forbes & Hemsley (1899) 26: 467, is *F. hiiranensis* Hayata, according to Hayata: *Icones plantarum Formosanarium* 8: 125. 1919; but should belong to *F. konishii* Hayata, in the opinion of Sata (1944) pt. I, 62, because its receptacles are clustered, and not axillary as in *F. hiiranensis*. Hayata and Sata say that *F. roxburghii* is not a native of Formosa.

SYNONYMY: VALID AND ALLEGED

The first description of this species was by J. E. Smith, who called it "*F. macrophylla* Roxb. & Buch. MSS." "Buch.", of course was short for Buchanan, also known as Francis Hamilton. Obviously this was the *F. macrophylla* Roxb. reported by Roxburgh (1814) 66 in his catalog of the plants in the East India Company's botanic garden in Calcutta, with the note that it came from Chittagong and had been introduced before 1793. Roxburgh's notes (1832) described *F. macrophylla* Roxb. in detail and listed Nepal, Sylhet (in Assam), and Chittagong as its distribution.

But *F. macrophylla* was not a valid name, for it had been given without description to an Australian tree by Desfontaines in 1804, and had been published by Persoon in 1807. Therefore Wallich, in his list of the plants in the museum of the East India Company (1831) no. 4508, bestowed the new name *F. roxburghii* upon two specimens: A, "*macrophylla* Hb Roxb. not Desfont."; and B, an unlabeled specimen from Hamilton's herbarium and the botanical garden of Calcutta. Wallich's title is valid, since it refers to a

species already validly described under a non-valid name, and has been accepted by most writers except Stewart (1869) 214, who ascribed the authorship to Miquel, and Haines (1924) 5: 839, who retained Roxburgh's *macrophylla*.

Here it may be noted that *F. macrophylla* Hort. Berol. ex Kunth (1846) 15 was stated by Kunth to be *F. anacardiifolia* Kunth & Bouché, and that *F. roxburghii* Miq. (1848) 7: 456 was cited by King (Ann.) 1: 171 as a synonym of *F. hirta* var. *roxburghii* (Miq.) King. The synonymy given by Stewart (above) shows that he did not refer to this variety.

Covellia macrophylla represents Miquel's attempt to place Roxburgh's species under a division of Ficus which now is considered a sub-genus. In (1867) 3: 296 he listed *C. macrophylla* under *F. roxburghii* Wall. The genus has been misspelled *Cerellia* by Watt (1890) 3: 361.

Griffith's species, whose name is spelled in different ways in his plate and in his text, has been cited under *F. roxburghii* by King (Ann.) and (1888) 5: 534, and by Gagnepain (1928) 5: 806. Both call it *F. scleroptera*. This is more important than a mere slip in orthography, since "hard-winged" is descriptive of no part of *F. roxburghii*. "Hard-fruited," however, is significant in connection with Griffith's statement that the fig is inedible, since Fairchild (above) says that the receptacles are woody until the female flowers are induced to mature. Griffith's text states that the species is allied to *F. macrophylla* Roxb., and his plate is a good representation of leaf, bud, and fig of *F. roxburghii*. *F. scleroptera* Miq. is *F. callosa* Willd. according to King (Ann.) 1: 64, and Gagnepain (1928) 5: 773.

Miquel's description of *F. regia* said that the leaves differed from those of *F. roxburghii* Wall. in the marginal teeth. But King, who examined type specimens, declared (Ann.) 1: 169 and 171 that *regia* was partly *roxburghii* and partly *F. pomifera* Wall. and that *F. regia* as described by Kurz (1877) 2: 459 was *F. pomifera* Wall. Gagnepain agreed with King's allocation of *F. regia* Miq. *F. pomifera* Kurz is *F. callicarpa* Miq., according to King (Ann.) 1: 69.

It is possible that some herbarium specimens thought to be *F. roxburghii* really belong to *F. pomifera* Wall. Therefore distinguishing characters of the latter are here listed: height to 18 m.; bark white, smooth; leaves lanceolate, elliptical or obovate-elliptical, with a base which is rounded or sub-cuneate, but never cordate; receptacles about 2.5 cm. in diameter, sometimes warty, with 4-6 vertical grooves; peduncles 1.3-4 cm. long, slender.

F. macrocarpa Lév. & Van. and "*F. Letacqui*" of the same authors were listed as synonyms of *F. roxburghii* by Handel-Mazzetti (1929) 7: 100. Both were described from "Kouy-Tchéou" (Kweichow), China. I have not seen the original text on *F. macrocarpa*, which Léveillé ascribed to Wight, but have read his description in Fedde, Repert. 4: 85. 1907. Rehder (1936) 17: 81, 82 declared *F. macrocarpa* Lév. & Van. (not Wight) a valid synonym but believed *F. letaqui*, described in Fedde, Repert. 8: 550. 1910, a different species because of its scabrid leaves, longer and slenderer petioles, and much smaller receptacles. Specimens of *F. letaqui* from Kweichow, *Y. Tsiang* 4315

and 7048, show slightly obovate blades 19 x 9 cm. in size, with a rather finely dentate margin and a somewhat narrowed base; and receptacles which are ovoid, warty, and measure 2.2 x 1.5 cm. On the card of one specimen the name had been corrected from *F. tsiangu* Merrill.

F. auriculata Lour. Fl. Coch.-Chin 2: 666. 1790, has been a doubtful and debated species for many years. Loureiro's descriptions in the first and second editions of his text are identical. That of the leaves corresponds well to *F. roxburghii*, and so does that of the figs as edible, turbinate, 5 cm. in size, smooth, red, with three basal bracts (called calyx by the author). Differences from *F. roxburghii* are in the large tree with oblique branches, and in the auriculate (eared) figs borne in crowded erect terminal racems.

The history of *F. auriculata* shows that it was quoted almost literally by early compilers. Rafinesque (1838) 59 changed its name to *Tremotis cordata*, but added nothing to Loureiro's text except the location Annam, in Indo-China. Miquel (1867) 3: 296 mentioned *F. auriculata* as a very doubtful species, and King (Ann.) 1: 179 stated that probably it was *F. cunia* Hamilt., but that he had not seen a specimen. This allocation seems strange, since King's plate 126 of *F. cunia* shows a narrow elliptical leaf with an extremely asymmetrical base, and a hairy, ribbed, sessile receptacle 1.5 x 1 cm. in size. Specimen *A. Henry* 12149 from Yunnan, China, agrees with this plate. No ears are visible.

In 1935 Merrill & Chun (F 1935) 2: 216 declared that *F. auriculata* Lour. was the earliest name for *F. roxburghii* Wall., and listed it from Hainan, from which Merrill previously (1927) 5: 66 had reported *F. roxburghii*. Merrill (Je 1935) 24^2: 137 based the identity of the two species on Loureiro's description, and added that some evidence was obtained also from Cây va, a vernacular name cited by Loureiro, and given by Gagnepain for *F. roxburghii* in Indo-China. He believed that Gagnepain had ignored *F. auriculata*.

In the original description of *F. auriculata* the tree habit is not that of *F. roxburghii*. The difference in fruiting habit is of no value, since, as Merrill explained, no species of *Ficus* has erect racemes. Loureiro, therefore, may have seen a detached cluster. The eared surface of the figs, however, is an important character. Loureiro had said that there were four foramina near the apex, stretching to the shoulders of the fig, each surrounded by a prominent cartilage so that they appeared like ears. Merrill said that the name *auriculata* came from the scales surrounding the ostiole. These two statements seem different to me. By foramina Loureiro may have meant the deep wrinkles which sometimes are seen radiating from the apex of a fig, especially when it has shrunk in drying. They may run as far as the beginning of the sides of a turbinate fig. Merrill apparently referred to the scales at the apex which almost completely cover the ostiole.

Neither statement fits *F. roxburghii*. The wrinkles, when present are not surrounded by ear-like cartilages; and the apical scales are usually small, somewhat heart-shaped, flat, and imbricated. Even when they are erect, as in Wight's plate (above), they do not resemble ears. Nor are they on the shoulders of the fig. It is true that some species of the sub-genus *Neomorphe*

bear lateral bracts or scales, and some of these are shown in Wight's plate, although they do not suggest ears and are not near the shoulders. They can not be common in *F. roxburghii*, for no one seems to have mentioned them. Of the herbarium specimens labeled *F. roxburghii* and *F. auriculata*, many of them from Hainan, only that of *S. K. Lau* 1391 had them, and in this specimen neither leaves nor figs were like those of *F. roxburghii*. It will be noticed, also, that Loureiro omitted the conspicuous vertical ridges of the receptacles, and the unusual places from which the figs are produced.

It is doubtful whether *F. roxburghii* would grow in Cochin-China, even under cultivation. King (Ann.) 1: 171 states that this species, in contrast to *F. pomifera* Wall., does not grow far south; and Fairchild says that it is not tropical, and is not found in gardens of Ceylon, Java, etc.

Vernacular names are not always a correct indication of the identity of species. Loureiro cited *Cay Ba(?)* for *F. auriculata*, the question mark indicating a rising inflection. Gagnepain listed *Cây va* for *F. roxburghii*, but *Cây vả* for *F. variegata* Blume. In several cases he stated the same vernacular name for several different species: ex. *Cay ngai*. This was cited on p. 776 for *F. heterophylla* L., on p. 809 for *F. variegata*, and on p. 812 for *F. hispida* L.f. Loureiro (1793) 819 put *Cây ngáy* under *F. maculata*.

Finally, Gagnepain (above) 5: 748 gave it as his belief that *F. auriculata* Lour. was not *Ficus*, but might be *Artocarpus* sp. Miquel (1867) 3: 296 had cited *Artocarpus imperialis* Hügel (in letters) as a synonym of *F. roxburghii* Wall.

SUMMARY

F. roxburghii Wall. is characterized by its spreading bushy habit, its very large roundish leaves, and its big top-shaped figs which are borne on the trunk, in the crotches of the lowest branches, and on root-like branches which rest on the ground at the base of the trunk. It is sub-tropical rather than tropical and is easily cultivated. Fertilization of the female flowers is induced by mechanical means rather than by pollination, according to Cunningham. Partly because of the place of the figs the species is placed under subgenus *Neomorphe*.

In addition to the original name, *F. macrophylla* Roxb. & Hamilt. ex Smith (not *F. macrophylla* Roxb., as it usually is written), other suggested synonyms are *Covellia macrophylla* (Roxb. & Hamilt.) Miq., *F. sclerocarpa* Griff. (misspelled *scleroptera* by King and others), *F. regia* Miq. (in part), *F. macrocarpa* Lev. & Van. (on the authority of Rehder), and *F. auriculata* Merr. & Chun. The last name indicates Merrill's belief that *F. auriculata* Lour. was the earliest name for this species, and that specimens from Hainan should be so entitled. But Gagnepain has declared that he believes Loureiro's species to be *Artocarpus* sp., and the original description of *F. auriculata* agrees with *F. roxburghii* only in the leaves.

It is possible that some specimens of *F. pomifera* Wall. have been thought to be *F. roxburghii*, although their leaves are ovate, and not cordate; and their figs are much smaller and on peduncles longer and slenderer in proportion.

REFERENCES

The last figure (or figures) after the title usually represents the volume-number. Additional titles are in the text.

AITON, WILLIAM 1789—Hortus kewensis, ed. 1, 3.

———1813—Hortus kewensis, ed. 2, 5.

ALSTON, A. H. G. 1931—Supplement to Trimen, H. A hand-book to the flora of Ceylon.

BAILEY, F. M. [1913] Comprehensive catalog of Queensland plants.

BARRETT, M. F. (see introduction).

BEDDOME, R. H. 1874—The flora sylvatica for southern India 2.

BENTHAM, G. 1861—Flora hongkongensis.

BLUME, K. L. 1823—Catalogus van eenige—gewassen—te Buitenzorg.

———1825—Bijdragen tot de Flora van Nederlandsch Indië.

———1836—In Rumphia 2.

BOERHAAVE, HERMAN 1710—Index plantarum quae in horto academico lugduno-batavo reperiuntur.

———1720—Index alter plantarum quae in horto academico lugduno-batavo aluntur.

BRANDIS, DIETRICH 1874—Forest flora of north-west and central India.

———1906—Indian trees.

BREITER, C. A. 1817—Hortus breiterianus.

COMMELIN, JAN ed. 1682—Rheede, Hort. Mal. 3.

COMMELIN, KASPAR 1696—Flora malabarica.

COOKE, THEODORE 1907—The flora of the Presidency of Bombay 2.

CORNER, E. J. 1933—A revision of the Malayan species of *Ficus: Covellia* and *Neomorphe*. Jour. Malayan Roy. Asiat. Soc. 11.

COWAN, A. M. & J. M. 1929—The trees of northern Bengal.

DECAISNE, JOSEPH 1834—Description d'un herbier de l'île de Timor. Nouv. Ann. Mus. Hist. Nat. 3.

DE VRIESE, W. H. 1847—Description et figures des plantes nouvelles et rares du Jardin botanique de l'université de Leide—fasc. 1.

DRURY, HEBER 1869—Handbook of the Indian flora 3.

DUNN, S. & TUTCHER, W. 1912—Flora of Kwantung and Hongkong. Kew Bull. Misc. Inf. Add. Ser. X.

DUTHIE, J. F. 1915—Flora of the Upper Gangetic Plain—3.

ELMER, A. D. E. —Leaflets of Philippine botany 1: 10 Ap 1906; 7: 25 Ag 1914; 9: 1937.

FISCHER, C. E. C. 1928—Flora of the Presidency of Madras 8.

FORBES, F. B. & HEMSLEY, W. B. 1899—An enumeration of all the plants known from China—(Index florae Sinensis). Jour. Linn. Soc. 26.

FORBES, H. O. 1925—Malayan plants. Jour. Bot. 63: suppl.

GAGNEPAIN, FRANÇOIS 1928—Moracées. In Lecomte, P. H. Flore générale de l'Indo-Chine 5.

GASPARRINI, GUILIELMO 1844—Nova genera quae super nonnullis fici speciebus.

———1845—Richerche sulla natura del caprifico, e del fico, e sulla caprificazione. Rendic. Acad. Sci. Napoli 4.

GRAHAM, JOHN 1839—A catalogue of the plants of Bombay.

GRIFFITH, WILLIAM 1848—Itinerary notes 2, 3.

———1854a—Icones plantarum asiaticarum.

———1854b—Notulae ad plantas asiaticas 4.

HAINES, H. H. 1924—The botany of Bihar and Orissa pt. 5, 6.

HAMILTON, FRANCIS (BUCHANAN-HAMILTON)—A commentary on the *Hortus Malabaricus* pt. 1, pt. 3. In Trans. Linn. Soc. Lond. 13, 15. 1822, 1827.

HANDEL-MAZZETTI, HEINRICH 1929—Moraceae. Symb. Sin. 7.

HERMANN, PAUL 1717—Musaeum zeylanicum.

HUNGER, F. W. T. 1918—Boerhaave comme naturaliste. Janus 23.

JONES, WILLIAM 1795—Botanical observations on select Indian plants. Asiat. Research 4.

KING, GEORGE 1887-1888—The species of *Ficus* of the Indo-Malayan and Chinese countries. Ann. Bot. Gard. Calcutta 1.
———1888—*Ficus*. In Hooker, J. D. Flora of British India.
KOORDERS, S. H. 1912—Excursionsflora von Java 2.
——— & VALETON, THEODORIC 1906—Boomsorten op Java 11.
——— & ———1916-1918—Atlas der Baumarten von Java.
KUNTH, C. 1846—Enumeratio synoptica *Ficus* specierum—horti regii botanici berolinensis. In, Index seminum horti berolinensis 1846.
———1847—*Ibid*. Ann. Sci. Nat. III, 7.
KURZ, SULPIZ 1877—Forest flora of British Burma 2.
LAMARCK, J. B. A. P. 1788—Encyclopédie méthodique 2.
LÉVEILLÉ, HECTOR 1907—In, Memorias de la academia de ciencias y artes Barcelona.
———1907b-1911—Decades plantarum novarum. Fedde, F. D. G. Repertorium specierum novarum regni vegetabilis 4, 6, 8, 9.
———1914—Plantes insignes du Kouy-Tchéou. Bull. Geog. Bot. 24.
———1915—Flore du Kouy-Tchéou.
LINK, H. F. 1822—Enumeratio plantarum horti regii berolinensis 2.
LINNAEUS, CAROLUS 1737—Hortus cliffortianus.
———1747, 1748—Flora zeylanica ed. 1, ed. 2.
———1749—Amoenitates academicae 1. 1759-4.
———1753, 1763—Species plantarum ed. 1, ed. 2.
———1767-1771—Mantissa plantarum.
———1777—Pflanzensystem 2. (Houttuyn ed.)
LOUREIRO, JUAO 1790, 1793—Flora cochinchinensis 2, ed. 1, ed. 2.
MACMILLAN, H. F. 1935—Tropical gardening and planting.
MERRILL, E. D. N 1917—An interpretation of Rumphius' Herbarium Amboinense. Dept. Agr. Bot. Sci. Publ. 9.
———1918—Species blancoanae.
———1923—An enumeration of Philippine flowering plants 2.
———1927—An enumeration of Hainan plants. Lingnan Sci. Jour. 5.
———1935—A commentary on Loureiro's "Flora Cochinchinensis." Trans. Am. Philos. Soc. new ser. 24, pt. 2.
——— & CHUN, W.-Y. F 1935—Additions to our knowledge of the Hainan flora. Sunyatsenia 2.
MILLER, PHILIP 1731, 1759, 1768—The gardener's dictionary, ed. 1, 7, 8.
———1807—Gardener's and botanist's dictionary. (Martyn ed.)
MIQUEL, F. A. W. 1847, 1848—Prodromus monographiae ficuum. Hook. Lond. Jour. Bot. 6, 7.
———1853—Plantae Iunghuhnianae, fasc. 1.
———1854—(*Ficus, Urostigma,* and *Covellia*) in Zollinger, Heinrich. Systematisches Verzeichneiss der im Indischen Archipelgesammelten Pflanzen.
———1859—Flora indiae batavae 1 (2).
———1860—Flora indiae batavae, supplementum primum.
———1866-1867—Prolusio florae japonicae. Ann. Mus. Bot. Lugd.-Batavi 2.
———1867—Annotationes de *Ficus* speciebus. Ann. Mus. Bot. Lugd.-Batavi 3.
MOWRY, HAROLD 1938—Ornamental trees. Fla. Agr. Exp. Sta. Ext. Bull. 95.
NEHRLING, HENRY 1944—My garden in Florida 1. (A. H. Andrews, ed.)
NORONHA, FERNANDO 1790—In Verh. Bat. Gen. 5.
PERSOON, C. H. 1807—Synopsis plantarum 2.
PLUKENET, LEONARD 1692-1696—Phytographia.
———1696—Almagestum botanicum.
POIRET, J. L. M. 1812—Encyclopédie méthodique. Botanique. Supplément 2.
RAFINESQUE-SCHMALTZ, C. S. 1838—Sylva telluriana.
REHDER, HENRY—Notes on the ligneous plants described by H. Léveillé from Eastern Asia. Jour. Arnold Arb. 10. 1929. 17. 1936.
———1940—Manual of cultivated trees and shrubs.
RHEEDE, H. A. VAN R. TOT D. 1678—Hortus indicus malabaricus. Pt. 1. 1682, Pt. 3.

RIDLEY, H. N. 1924—The flora of the Malay Peninsula 3.
ROBINSON, C. B. 1912—Roxburgh's Hortus Bengalensis. Philipp. Jour. Sci. C. Bot. 7.
ROEMER, J. J. & SCHULTES, J. A. 1817—ed. Linnaeus, Systema vegetabilium 1.
ROTH, A. W. 1821—Novae plantarum species.
ROXBURGH, WILLIAM 1798—Plants of the coast of Coromandel 2.
———1814—Hortus bengalensis.
———1832—Flora indica, ed. 2, 3. Later ed. 3, 1874.
ROYAL PALM NURSERIES, ONECO, FLORIDA (1938)—Tropical planting book.
RUMPHIUS, ADRIAN VAN 1743, 1755—Herbarium amboinense 3, 6.
SALISBURY, R. A. 1796—Prodromus stirpium in horto ad Chapel Allerton vigentium.
SATA, NAGAHARU (TYOSYUN) 1944—A monographic study of the genus *Ficus* from the point of view of economic botany. Contr. Inst. Hort. & Econ. Bot. Taihoku Univ. 32.
SAVAGE, SPENCER 1945—A catalogue of the Linnaean herbarium. Linn. Soc. London.
SCHNEIDER, CAMILLO 1916—*Moraceae.* In, Sargent, C. S. ed. Plantae Wilsonianae 3 (2).
SENN, ERNEST 1912—In, Karsten, Georg & Schenck, Heinrich, Vegetationsbilder 10 (4).
SIMPSON, C. T. (1926)—Ornamental gardening in Florida.
SMALL, J. K. 1933—Manual of the southeastern flora.
SMITH, J. E. 1810—*Ficus.* In, Rees, Abraham. Cyclopaedia 14 (2).
SPRENGEL, K. P. J. ED. 1826—Linnaeus, Systema vegetabilium 3.
STEUDEL, E. G. 1821, 1840—Nomenclator botanicum ed. 1, ed. 2, 1.
STEWART, J. L. 1869—Punjab plants.
STOKES, JOHNATHAN 1812—A botanical materia medica.
STURROCK, DAVID & MENNINGER, EDWIN A. [1946]—Shade and ornamental trees for south Florida and Cuba.
SWEET, ROBERT 1818—Hortus suburbanus londinensis.
SYEN, ARNOLD. 54.—See Rheede 1.
TAYLOR, NORMAN 1935—*Ficus.* In, Bailey, L. H. ed. Standard cyclopedia of horticulture.
THUNBERG, C. P. 1786—Dissertatio de *Ficus* genus.
THWAITES, G. H. K. 1864—Enumeratio plantarum zeylaniae.
TRIMEN, HENRY 1885—A systematic catalogue of the flowering plants and ferns—in Ceylon.
———1898—A hand-book to the flora of Ceylon 4. (See also Alston).
VAHL, MARTIN 1806—Enumeratio plantarum 2.
VIDAL Y SOLER, SEBASTIAN 1883—Sinopsis de familias y géneros de plantas leñosas de Filipinas.
———1885—Phanerogamae cumingianae philippinarum.
———1886—Revision de plantas vasculares filipinas.
VILLAR, COELESTINO FERNANDEZ 1880—Novissima appendix ad floram philippinarum. In, Blanco, Manuel. Flora de Filipinas ed. 3, 4.
VOIGHT, J. O. 1845—Hortus suburbanus calcuttemsis.
WALLICH, NATHANIEL 1831 (this part)—A numerical list of dried specimens of plants in the East India Company's museum. (Catalogue.)
WATT, GEORGE 1890—A dictionary of the economic products of India 3.
WIGHT, ROBERT 1843, 1853—Icones plantarum indiae orientalis 2, 6.
WILLDENOW, K. L. 1801—In, Acta Acad. Berol. 1796 (or 1798).
———1806—ed. Species plantarum 4.
———1809—Enumeratio plantarum horti regii berolinensis.
WILSON, GAINES R. 1938—Shade tree planting in southern Florida. Proc. Fla. Hort. Soc. 1937.
ZANONI, GIACOMO 1742—Rariorum stirpium historia.
ZEYHER, J. M. 1818—Verzeichniss der Gewächse im Grossherzoglichen Garten zu Schwetzingen.
ZOLLINGER, HEINRICH —See Miquel, 1854.

On the Cytotaxonomy of the genus Corydalis, Section Eucorydalis*

Gerald B. Ownbey
University of Minnesota, Minneapolis

The species of *Corydalis* found in North America are divided readily into three well-marked sections. Section *Pes-gallinaceous* is represented by a single diminutive arctic species, *C. pauciflora* (Steph.) Pers., native to northern Asia, Alaska, Yukon, and adjacent British Columbia. Section *Ramoso-sibiricae* is represented in North America by two species, *C. Scouleri* Hook. of western Washington and northwestern Oregon, and *C. Caseana* Gray which has several subspecies each of which has a more or less local distribution in the Rocky Mountains and Sierra Nevada. Section *Eucorydalis* is represented by seven species and several subspecies, and is found throughout North America. Several of its species, particularly *C. aurea* Willd. and *C. sempervirens* (L.) Pers. are very widely distributed geographically.

No materials of *C. pauciflora* or *C. Scouleri* have been available for this study. Seeds of all of the subspecies of *C. Caseana*, collected in 1946, failed to germinate when planted a year later. Due to these circumstances, attention in this study necessarily has been confined to the one section, *Eucorydalis*.

All of the chromosome counts here reported were made from root tips taken from plants grown from seed in the botany greenhouse, University of Minnesota and in the botany greenhouse, Washington University, St. Louis, Missouri. Root tips were killed and fixed in Karpechenko's modification of Navashin's fixative, embedded in paraffin, and sectioned at 9 microns. The sections were stained in safranin with a premordant of chromic acid and a postmordant of picric acid, then mounted in clarite.

Mitotic divisions of cells at metaphase where the chromosomes were well scattered at the equatorial plane were not difficult to find in the preparations. Chromosome counts for the species are summarized in the accompanying table. In each case identification numbers, collectors and collection numbers are also given. Validating specimens for all of the M. Ownbey & G. B. Ownbey collection numbers are to be found in the Herbarium of the Missouri Botanical Garden and in the Herbarium of the University of Minnesota as well as in other herbaria throughout the United States. Specimens of the remaining collection numbers, where extant, are deposited at the latter institution.

---

* This investigation was supported in part by a grant from the Graduate School, University of Minnesota, Minneapolis. The writer wishes to acknowledge assistance of Miss Carol Webb in the preparation of materials for study.

Species	Ident. no.	2n	Collectors and Collection numbers
C. aurea Willd. subsp. *aurea* G. B. Ownb.	C-18	16	M. Ownbey & G. B. Ownbey #3035
C. aurea subsp. *aurea*	C-19	16	M. Ownbey & G. B. Ownbey #3032
C. aurea subsp. *aurea*	C-20	16	F. G. Meyer, s. n.
C. aurea subsp. *aurea*	C-21	16	M. Ownbey & G. B. Ownbey #3055
C. aurea subsp. *aurea*	C-44	16	G. B. Ownbey #963
C. micrantha (Engelm.) Gray subsp. *micrantha* G. B. Ownb.	C-12	16	G. B. Ownbey, s.n.
C. micrantha subsp. *micrantha*	C-43	16	G. B. Ownbey #957
C. sempervirens (L.) Pers.	C-41	16	G. B. Ownbey #954
C. sempervirens	C-42	16	G. B. Ownbey #956

The exact localities where seeds and specimens of the collection numbers shown in the above table were procured are as follows: *C. aurea* subsp. *aurea*. C-18: On loose gravel pile 3.4 miles southwest of South Fork, Rio Grande Co., Colo., July 16, 1946. C-19: Disturbed soil, aspen woods, 14 miles northeast of Mancos, Montezuma Co., Colo., altitude about 9800 ft., July 14, 1946. C-20: In the Mogollon Mts., Catron Co., N. Mex., altitude about 8000 ft., 1947. C-21: Disturbed soil in gravel pit, 1 mile north of Almont, Gunnison Co., Colo., July 17, 1946. C-44: In sand near cabins, Univ. of Minnesota Forestry and Biological Station, Ithaca State Park, Minnesota, Aug. 6, 1948. *C. micrantha* subsp. *micrantha*. C-12: Sandy, frosted area, north slope near Pacific, Franklin Co., Mo., Dec. 20, 1941. C-43: On prairie "noses," bluff, south bank of Minnesota River just above Mendota Bridge, Dakota Co., Minn., May 20, 1948. *C. sempervirens*. C-41: Summit overlooking Moss Lake, Gunflint Trail, about 30 miles north of Grand Marais, Cook Co., Minn., May 30, 1948. C-42: In mossy crevices, Honeymoon Rock near Grand Marais, Cook Co., Minn., May 30, 1948.

It is apparent from the data presented in the table that the standard chromosome number for somatic cells is 16 for all North American members of the section *Eucorydalis* examined. The individual chromosomes were found to be almost identical morphologically in all species examined. They are short-cylindric in shape, being approximately 3-4 times greater in length than in diameter. There is, therefore, no cytological evidence to date which would indicate that this section is other than a natural group of genetically related species. As *C. sempervirens* differs morphologically from the mean for the section more than does any other American species included, it is of considerable interest to find that there are no observed cytological differences.

Because *C. aurea* is a highly polymorphic, widespread species, it seemed desirable to make comparative studies of this species from as many localities as feasible. It will be noted that chromosome counts were made from material from widely separated localities in Colorado, from New Mexico, and from Minnesota. C-19 from Montezuma Co., Colorado, represents a very vigorous race with very stout stems, large fruits, and broad ultimate leaf segments. This race was described as a separate species, *C. macrorrhiza* Fedde (Fedde, 1912). C-18, C-20, and C-21, respectively from Rio Grande Co., Colorado,

Catron Co., New Mexico, and Gunnison Co., Colorado, are somewhat less vigorous than C-19, the ultimate leaf segments are narrower and the fruits smaller. They represent the commonest type found in the Rocky Mountains. C-44 from Cook Co., Minnesota typifies the more northeastern facies of subspecies *aurea*, the most extreme forms of which differ in minor morphological details from the commonest Rocky Mountain form.

Both counts of *C. micrantha* were made from typical material of subspecies *micrantha*. This subspecies is relatively uniform morphologically throughout its range except in the Ozarks of Missouri where a recognizable variant occurs.

C. sempervirens is a morphologically uniform species lacking recognizable regional facies.

So far as I am aware, these are the first chromosome numbers reported for North American species of *Corydalis*. A few counts have been reported for European species, and these have been summarized by Darlington & Janaki (1945) and by myself (Ownbey, 1947). The basic number in the European species reported is 8 with one possible exception where it may prove to be 7. Somatic counts reported are 16, 24, and ?56.

It is especially pertinent to a more complete understanding of the cytotaxonomic picture of *Corydalis* in North America that chromosome counts be made of other species, especially of the subspecies of *C. Caseana* and of the monotypic *C. Scouleri* and *C. pauciflora*. Judging entirely on the basis of the morphologic distinctness of these species, it seems most likely that if any deviations from the diploid number of 16 occur in North American species, it is most likely to occur here. Further, attempts to accomplish artificial crosses between species and subspecies of the section *Eucorydalis* would furnish data on the strength of the sterility barriers between the various species.

SUMMARY

Cytological examination of root tip preparations of five collections of *C. aurea* subsp. *aurea*, two collections of *C. micrantha* subsp. *micrantha*, and two collections of *C. sempervirens* established the chromosome number for somatic cells of all three as 16. This indicates that the section *Eucorydalis* to which all three species belong is probably a natural group insofar as the North American speceis are concerned. Desirability for further investigation of North American species of section *Eucorydalis*, and especially of the North American representative of the section *Ramoso-sibiricae* and *Pes-gallinaceous* is indicated.

REFERENCES

DARLINGTON, C. D. AND E. K. JANAKI 1945—Chromosome atlas of cultivated plants. P. 69.

FEDDE, F. 1912—Neue Arten aus der Verwandtschaft der *Corydalis aurea* Willd. von Nord-Amerika. V. Rep. Spec. Nov. 10: 479-480.

OWNBEY, G. B. 1947—Monograph of the North American species of *Corydalis*. Ann. Mo. Bot. Gard. 34: 187-260.

An Ecological Survey of the Fort Leavenworth Military Reservation*

Malcolm J. Brumwell*

Department of Zoology, University of Kansas, Lawrence

CONTENTS

Introduction 187
Historical 187
Physiography 188
Drainage 188
Climate 190
Biotic relationships 190
Ecological associations 193
I. Grant Hill, Engineer's Hill and vicinities 193
II. Government Hill, North Hill and vicinities 196
III. Sherman Field and vicinity 198
Annotated list of amphibians 200
Annotated list of reptiles 203
Annotated list of mammals 208
Annotated list of birds 214
Acknowledgments 229
Conclusions 230
References 230

Introduction

This survey was undertaken to determine the relationships between the amphibians, reptiles, birds and mammals and the various factors of their environment. The Fort Leavenworth Military Reservation provides an area sufficiently untouched by man to assure the existence of natural conditions over considerable areas. McColloch (1926) lists Fort Leavenworth as one of the natural areas of Kansas.

The fact that a similar study for the Doniphan Lake Area in the Missouri River Valley about 23 miles north of Fort Leavenworth, has been reported upon (Linsdale, 1927, 1928a, 1928b, 1928c, 1933) affords opportunity for comparison of similar areas after an interval of fifteen years. My work was done from January, 1939, to November, 1940.

Rydberg's (1932) *Flora of the Prairies and Plains of Central North America* was used, whenever possible, to identify plants; otherwise Britton and Brown's (1936) *An Illustrated Flora of the United States and Canada* was consulted. All specimens of vertebrates collected were placed in the Museum of Natural History at the University of Kansas.

Historical

In 1804 Lewis and Clark reported, of their journey along the river near the present site of Fort Leavenworth, "Pecan trees were this day seen and large quantities of deer and wild turkey," (Hunt & Lorence, 1937). They noted also an old French fort near the mouth of what is now known as Salt

* Published posthumously. Lieutenant Brumwell died December 14, 1941, as a result of injuries incurred during the Japanese attack on Pearl Harbor. This paper is a condensed version of his thesis for the Master's degree.—A. Byron Leonard and E. Raymond Hall.

Creek at the northwest edge of the present site of Fort Leavenworth. Although the abundance of game and rich vegetation there was attractive to early explorers, malaria discouraged early settlement and it was not until much later that the region was inhabitable during the summer months.

The reservation contains 5842.31 acres. Of this, the 1800 acres used by the Leavenworth Federal Penitentiary were unavailable for my study. The approximate area included in this survey is 4042 acres.

PHYSIOGRAPHY

The Fort Leavenworth Military Reservation lies completely within the glaciated plains. Much of the land is glacial drift and windblown loess which forms a rich sandy silt. Elevations above mean sea level range from 740 feet at low water to more than 1083 feet on Government Hill and accessory ridges. The upland slopes slightly to the east.

The Pennsylvanian series of the Carboniferous system of rocks outcrops here. The indurated strata of Pennsylvanian Age are overlain in most places by unconsolidated till and windblown loess of Pleistocene Age and in lower areas by alluvium of Recent times. Beneath is a great thickness of Paleozoic strata resting on granite. The order of the formations from the Missouri River to the westward is alluvium, Weston Shale, Lawrence Shale, Oread Limestone and glacial drift; windblown loess is found only on North Hill.

Erosion of the consolidated rocks, both before and after glaciation, produced more or less conspicuous escarpments capped by the resistant Oread Limestone and rolling plains on non-resistant rock. The Oread Escarpment, a strong topographic feature 150-340 feet high, forms steep slopes bounding Pilot Knob, Government Hill and other narrow, irregular-shaped ridges west of the Missouri River. The exceptionally high ridges north of Bear Creek and east of the river are of the same formation.

A beautiful view of the broad valley of the Missouri River and Fort Leavenworth may be obtained from these ridges.

The topography of the territory adjacent to the flood plains of the Missouri River owes its character, in part, to the thick accumulation of loess along the bluffs; rapid erosion down to the till is noticeable wherever the loess is present and has formed miniature canyons.

The flood plain of the Missouri River is a broad fan-shaped, alluvial deposit formed in the bend of the river to the east. This alluvium reaches a maximum depth of 57 feet; the elevation varies from 740 feet at low water to 790 feet near the western border along the mainland (Hinds and Greene, 1917).

DRAINAGE

The drainage is entirely to the Missouri River which flows south 30 degrees east with a gradient of 0.8 feet per mile. The estimated mean discharge per year is 71,030 cu. ft. per second; this varies from 16,200 cu. ft. per sec. in December to 236,000 cu. ft. per sec. in July. In this same period 567,500 tons of suspended matter were carried per 24 hours. The range

between high and low water at Fort Leavenworth is 28.2 feet. The steep stream banks are from 20 to 30 feet high.

The channel frequently shifts and many oxbow lakes, sloughs, and marshes are left to be slowly filled with silt during floods, and with vegetation during the recession of the waters. The general tendency of the river is to hug the right or west bluff, except at Fort Leavenworth where the river makes a huge loop, 1¼ to 1½ miles broad to the east.

Tributaries consist of Three Mile Creek (in part), Corral Creek, One Mile Creek, Quarry Creek, and Plum Creek and Salt Creek in part. The upper

PLATE 1.—The upper photograph shows the typical Symphoricarpos-sumach association to the right center. The ranges of the forest and prairie dwellers overlap in this type of a formation. Below is the prairie association of Grant Hill-Engineer Hill vicinity. This is the habitat of the meadow mouse: the grass in the background has been mowed and is the habitat favored by the striped spermophile.

courses of these streams gradually merge into the rolling uplands; the lower courses have well-developed alluvial flood plains and complex meanders (Hinds & Greene, *op. cit.*).

CLIMATE

The Kaw Valley Biotic District has a sub-humid, mesothermal climate, the precipitation being adequate at all seasons (VanDersal, 1938).

A meterological summary has been prepared for four stations: Fort Leavenworth; St. Joseph, Missouri; Kansas City, Missouri; and Topeka, Kansas. This gives roughly a fifty-mile range to the north, south, east and west.

The normal annual precipitation for St. Joseph, Fort Leavenworth, Kansas City and Topeka is 35.56, 35.50, 37.11 and 33.55 inches respectively.

In June, 1940, two hundred and eighty relative humidities were obtained with a sling psychrometer. All readings were taken on clear days, with not more than a slight breeze blowing, between the hours of 8:00 a.m. and 5:30 p.m. The mean reading for each association is shown below.

Association	Temp.	Rel. Humidity
Prairie	84	53.7%
Symphoricarpos-sumach	80.3	56.6
Sedge-willow	82.4	57.7
Cottonwood-elm	78.6	64.5
Oak-hickory	78.6	68.1

The climate at Fort Leavenworth is more stable than that at any one of the other three stations. The temperature is slightly higher and the relative humidity considerably greater, although it is evident from the data available that climatic conditions are more stable in a north-south direction than they are from east to west.

Each change of one degree Fahrenheit usually produces a corresponding variation, but in the opposite direction, of one and five-tenths to more than two per cent in relative humidity (Weaver & Clements, 1938: 335). Judging from the table above, temperatures in the various associations vary importantly; yet the corresponding variation in relative humidity is more than two per cent.

BIOTIC RELATIONSHIPS

Kansas is almost completely within the Upper Austral Life-zone (Merriam, *et al*, 1910) except for the southeastern and southcentral countries where the Lower Austral Life-zone intrudes several miles into the state.

The Missouri River Valley forms a huge corridor through which the Central Hardwood Forest extends westward, through the tall grass plains, into the mixed grass regions. From this corridor the flora and fauna of the deciduous forest complex have spread up the stream valleys of northeastern Kansas for many miles.

Kaw Valley Biotic District.—The flora of this district is characteristic of the eastern deciduous forest, oak-hickory-walnut and elm-cottonwood associations.

The characteristic mammals are the flying squirrel, *Glaucomys volans*

volans, short-tailed shrew, *Blarina brevicauda brevicauda*, thirteen-lined ground squirrel, *Citellus tridecemlineatus tridecemlineatus*, western harvest mouse, *Reithrodontomys megalotis dychei*, Florida cottontail, *Sylvilagus floridanus mearnsii*, chipmunk, *Tamias striatus griseus;* the typical *amphibians* are, *Hyla crucifer, Triturus viridescens louisianensis*, and *Ambystoma maculatum*.

Cherokee Prairie Biotic District.—This is the northward extension of the same district from Oklahoma (Blair and Hubbel, 1938). The plant associations are similar.

The mammals include the short-tailed shrew, *Blarina brevicauda hulophaga*, chipmunk, *Tamias striatus venustus*, Florida wood rat, *Neotoma floridana attwateri*, swamp rabbit, *Sylvilagus aquaticus aquaticus*, and the rice rat, *Oryzomys palustris texensis*. *Terrapene carolina trianguis*, and the snake, *Storeria occipitomaculata*, are the only reptiles typical of the district.

Ozark Biotic District.—This district enters the extreme southeastern corner of the state for a short distance, the major portion of this district lying in Oklahoma and Arkansas. The mammals include the golden harvest mouse, *Reithrodontomys fulvescens aurantius*, chipmunk, *Tamias striatus venustus*, brush mouse, *Peromyscus boylii attwateri*, muskrat, *Ondatra zibethicus zibethicus*. The typical amphibians are *Eurycea multiplicata, E. melanopleura* and

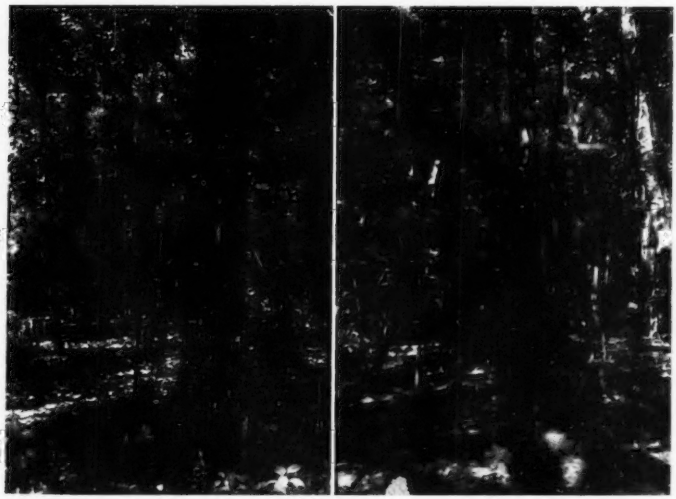


PLATE 2.—To the left is the cottonwood-elm forest near Corral Creek. The large tree is a cottonwood, the others are elms. The Sherman Field forest is shown on the right. The oak-hickory forms such a dense canopy that little undergrowth survives. The tree in the center is about two feet in diameter. This habitat is occupied by the gray squirrel, chipmunk, northern deer mouse, and cottontail rabbit; birds found here include many flycatchers, owls, broad-winged hawks, and occasionally an over-bird.

Typhlotriton spelaens. *Potamophis striatulus* and *Agkistrodon piscivorus* are typical reptiles.

Osage Savanna Biotic District.—For a short distance northward this district is typical of that part of the district lying in Oklahoma. The mammalian fauna is the same as in the part of the district lying in Oklahoma (Blair and Hubbel, 1938: 433-34, 450).

In Kansas the rainfall decreases almost 8 inches from that farther south and the flora consists of tall and mixed grasses with the admixture of many shrubs, forming a connection between the deciduous forest and the mixed grass plains. The white-footed mouse, *Peromyscus leucopus noveboracensis*, meadow mouse, *Microtus ochrogaster*, pine vole, *Pitymys nemoralis*, and the Florida wood rat, *Neotoma floridana osagensis* are common throughout; but in the northern half of the district the deer mouse, *Permyscus maniculatus bairdii*, pocket gopher, *Geomys bursarius* and Florida cottontail, *Sylvilagus floridanus mearnsii* are found. *Sylvilagus floridanus alacer* and the hispid cotton rat, *Sigmodon hispidus texianus*, range throughout the southern third of the district.

Mixed Grass Plains Biotic District.—The broad prairie lying between the Osage Savanna and the short grass plains extends from Oklahoma north into Nebraska. It consists of mixed grasses with occasional "islands" of forest and short grass formations.

The district has been subdivided into associations, the boundary being drawn arbitrarily somewhat north of the Arkansas River.

(a). The northern mixed-grass association is characterized by the following mammals: thirteen-lined ground squirrel, *Citellus tridecemlineatus tridecemlineatus*, deer mouse, *Peromyscus maniculatus bairdii* and *Peromyscus m. nebrascensis*, pocket gopher, *Geomys bursarius* and Florida cottontail, *Sylvilagus floridanus mearnsii*.

(b.) The southern mixed-grass association has more of the fauna and flora which occur in Oklahoma. Probably the lower Arkansas River Valley should not be included in this biotic district; it is undoubtedly a corridor from a more mesophytic district. The mammals found here are the plains wood rat, *Neotoma micropus micropus*, northern grasshopper mouse, *Onychomys leucogaster breviauritus*, white-footed mouse, *Peromyscus leucopus aridulus*, pocket gopher, *Geomys breviceps llanensis*, and thirteen-lined spermophile, *Citellus tridecemlineatus texensis*. The snake *Leptotyphlops myopica* is found here. The black-tailed jackrabbit, *Lepus californicus melanotis*, ranges throughout the association.

Short-Grass Biotic District.—This biotic district extends across the western third of Kansas from Oklahoma into Nebraska. It has been divided into northern and southern associations. No attempt has been made to designate the many sand hills and other areas of special biotic significance. Future investigation may show that the northwestern corner of the state is not to be included in this biotic district.

The southern association is typical of the Oklahoma short-grass plains (Blair and Hubbel, 1938: 440-441). The mammalain fauna includes the mole, *Scalopus aquaticus intermedius,* long-tailed weasel, *Mustela frenata neomexicana,* badger, *Taxidea taxus berlandieri,* Audubon cottontail, *Sylvilagus audubonii neomexicanus,* pocket gopher, *Geomys lutescens jugossicularis,* large spotted ground squirrel, *Citellus spilosoma major,* 13-lined ground squirrel, *Citellus tridecemlineatus arenicola,* deer mouse, *Peomyscus maniculatus osgoodi,* white-footed mouse, *Peromyscus leucopus tornillo,* and the woodrat, *Neotoma micropus canescens.* The lizard, *Sceloporus undulatus garmani,* and the toad, *Bufo insidior* are found here.

The mammalian fauna of the northern association is decidedly different and includes the following: spermophile, *Cittelus obsoletus,* 13-lined ground squirrel, *Citellus tridecemlineatus pallidus,* striped skunk, *Mephitis mephitis varians,* deer mouse, *Peromyscus maniculatus nebrascensis,* Florida wood rat, *Neotoma floridana campestris,* prairie vole, *Microtus ochrogaster haydenii,* porcupine, *Erethizon dorsatum bruneri,* white-tailed jackrabbit, *Lepus townsendii companius,* Florida cottontail, *Sylvilagus floridanus similis,* Audubon cottontail, *Sylvilagus auduboni baileyi,* and mole, *Scalopus aquaticus caryi.* These mammals range throughout the major part of this association.

Between the biotic districts of Oklahoma and Kansas there is much meterological difference. Although this difference is reflected in the flora, its significance in the fauna is less apparent.

ECOLOGICAL ASSOCIATIONS

Fort Leavenworth, in the Kaw Valley Biotic District, is identical with the Central Hardwood Forest. Clearing of most of the level land resulted in the establishment of communities of tall and mid-grasses which are typical of the Osage Savanna.

Classification into natural areas has been made according to the predominance of representatives of one biotic district or the other. The type of flora is the indicator of the existing meterological and soil conditions (Weaver and Clements, 1938: 454-465).

I. GRANT HILL, ENGINEER'S HILL AND VICINITIES

This area includes approximately 1354 acres, consisting of rolling prairie, Andropogon-Poa association, and wooded streams, cottonwood-elm associations. It occupies a position between the alluvial plain and the escarpment in the west, the elevation ranging from 800 feet, near the Missouri River, to approximately 900 feet at the bases of Government Hill and Cemetery Ridge (Plate I).

Prairie Association.—The prairie community is composed of tall and mid-grasses; among the more common are big blue stem, *Andropogon furcatus* Muhl., little blue stem, *Andropogon scoparius* Michx., western wheat grass, *Agropyron smithii* Rydb., and Kentucky blue grass, *Poa pratensis* I In the more mesic region, Indian grass, *Sorghastrum nutans* (L.) Nash, and Johnson grass, *Sorghum halapense* (L.) Pers. form abundant societies.

Due to heavy grazing (Weaver & Clements, 1938: 469-472), some of the prairie has been invaded by the milkweeds, *Asclepias syriaca* L., *A. sullivantii* Engelm. and *A. kansana* Vail, the daisy flea-banes, *Erigeron annus* (L.) Pers. and *E. ramosus* (Walt.), B. S. P., the yarrows, *Achillea millefolium* L. and *A. lanulosa* Nutt., the broad-leaved gum plant, *Grindelia squarrosa* (Pursh.) Dunal. and Baldwin's iron-weed, *Veronia interior* Small.

The slender, showy goldenrod, *Solidago rigidiuscula* (T. & G.) Porter and *Solidago glaberrima* Martens, are common on the prairie during late summer. The white heather aster, *Aster ericoides* L., is conspicuous in the autumn.

Among the more common plants that often form societies in this region and in the adjoining open woods and thickets are: quack grass, *Agropyron repens* (L.) Beauv., brome grass, *Bromus japonicus* Thunb., green bristle grass, *Setaria viridis* (L.) Beauv., orchard grass, *Dactylis glomerata* L., wild redtop, *Panicum virgatum* L., large crab-grass, *Digitaria sanguinalis* (L.) Scop., purple love grass, *Eragrostis pectinacea* (Michx.) Nees., love grass, *Eragrostis cilianensis* (All.) Link., warty spruge, *Poinsetta cuphusperma* (Boiss.) Small, Roman wormwood, *Ambrosia elatior* L., and ragweed, *Ambrosia striata* Rydb.

COTTONWOOD-ELM ASSOCIATION.—Corral Creek traverses the south half of the area from west to east and the drainage of Merritt Lake and One Mile Creek occupy the northern half. Both creeks form shallow gullies which afford ample protection and moisture for a heavy growth of trees and shrubs. From the edges of this growth the more mesophytic inhabitants advance outward into the prairie. In the dry years, up to and including 1939, many shrubs and a few trees which had become established on the prairie died.

The forest along the stream courses and gullies is mainly river poplar, *Populus deltoides* Marsh, American, or white elm, *Ulmus americana* L., sycamore, *Plantanus occidentalis L.*, white swamp oak, *Quercus bicolor* Willd., pin oak, *Quercus palustris* Muench. and soft maple, *Acer saccharinum* L.

The trees which are as much as eighteen inches in diameter at the height of a man's breast (18" D.B.H.) are mostly poplar, elm and sycamore; there are a few scattered oaks of this size. In a heavy growth of timber an 8 meter quadrat was marked off and the trees within it counted. The quadrat contained one cottonwood, 18" D.B.H., and 8 elms 5" D.B.H.

The most numerous vines and undershrubs are poison ivy, *Toxicodendron radicans* (L.) Kuntze, Virginia creeper, *Psedera quinquefolia* (L.) Greene, riverside grape, *Vitis vulpina* L., greenbrier, *Smilax hispida* Muhl., bittersweet, *Celastrus scandens* L., the touch-me-nots, *Impatiens nortonii* Rydb., and *I. pallida* Nutt., violet, *Viola papilonacea* Pursh., and Wright's sedge, *Carex* sp.

Much of the timber has a heavy tangled undergrowth which often forms an almost impenetrable mass of vegetation. Thus there is ample protection and food for many species of mammals and birds.

Symphoricarpos-Sumach Association.—This association occupies the transitional zone between the cottonwood-elm and the prairie communities. It

varies in width from three to one hundred yards. Its width usually depends upon the amount and type of recent disturbance of the soil. The association is characterized by the admixture of representatives of both prairie and forest communities and numerous species of weedy annuals and perennials. The growth is typical of the brush type, being dense and vigorous and provides food ample both in quantity and variety, for an abundant fauna (Leopold, 1937: 254-255).

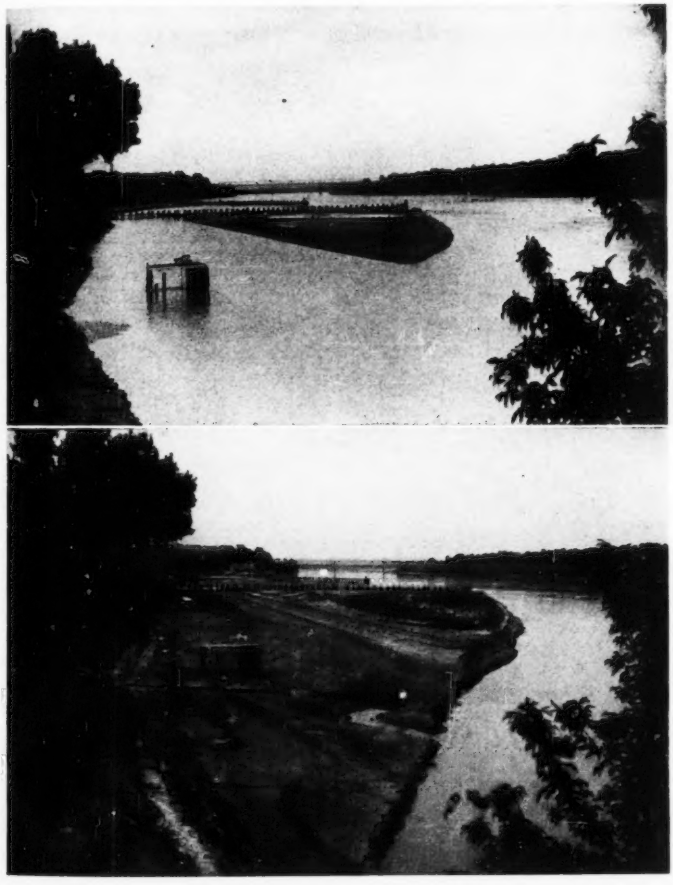


PLATE 3.—Two stages in the formation of a river sandbar. The upper photograph was taken during May, the lower during August, 1939. Except for an occasional cottontail rabbit, opossum and raccoon, no mammals were found. The American toad, leopard frog, soft-shelled turtle, and water snake were common.

Littoral Association.—This community consists largely of the banks and sandbars along the Missouri River, and the two small lakes, Merritt Lake and Smith Lake. The sandbar recently deposited along the Missouri River opposite Grant Hill is from fifty to one hundred and fifty yards wide and approximately 350 yards long. The sand is completely flooded for a few days each spring. During the season of 1939 most of the sandbar was covered by yellow cyperus, *Cyperus flavescens* L., shining cyperus, *Cyperus rivularis* Kunth, sedge, *Cyperus rotundus* L., dock-leaved persicaria, *Persicaria lapathifolium* (L.) S. F. Gray, pink smart week, *Persicaria coccinea* (Muhl.) Greene, field horsetail, *Equisetum arvense* L., yellow water cress, *Rorippa sinuata* (Nutt.) Hitchc., sessile-flowered cress, *R. sessiliflora* (Nutt.) Hitchc., and smooth creeping love grass, *Eragrostis hypnoides* (Lam.) B.S.P. On a meter quadrat, marked off in the above type of growth, a count of the individual plants yielded 32 of grass, 2 of sedge, 1 of small willow, 5 of pigweed and 1 of seapurslane.

In the season of 1940 the aspect of the sandbar was greatly changed due to a predominance of the cottonwood, *Populus deltoides* Marsh, and the willows, including *Salix missouriensis* Beb., and *S. interior* Rowlee. Golden dock, *Rumex persicarioides* L., and great water dock, *R. britannica* L., form dense societies in this habitat. A one meter quadrat marked off in the area dominated by poplar yielded 22 poplar saplings, 2 willows and 1 sedge.

A small pond, which was isolated on this sandbar by the recession of the water, was seined in September, 1940. This yielded: carp 489, minnows 1398, gar pike 2, bullhead 2, blue channel cat 5, perch 196, bluegill 71, bass 3. All except the gar pike were of fingerling size; the gar pike were 14 and 16 inches long.

Merritt and Smith lakes form the source of One Mile Creek. They are approximately equal in size and have a combined area of approximately 9½ acres. The depth of the water varies from a few inches to 20 feet. They are surrounded by prairie with here and there an isolated tree or clump of bushes. Repeated oiling of these waters in the summer seriously interfered with the vegetation. Mosquitoes are more efficiently controlled by the introduction of top minnows.

In August, 1940, these lakes were seined by the Leavenworth County Fish and Game Development Association (Honeycutt, 1940); approximately 1500 pounds of rough fish were taken from the two lakes; the largest fish was a buffalo weighing 36 pounds.

Smith Lake is well stocked with crappie and has a "sprinkling" of bass; Merritt Lake contains practically no game fish.

II. GOVERNMENT HILL, NORTH HILL AND VICINITIES

The escarpment bordering the reservation on the west is composed of Government Hill, Cemetery Ridge and North Hill; the relief extends from 900 feet to 1083 feet. The exposure is mostly eastward, an equal amount being to the north and south together. The approximate area is 1242 acres.

Three associations are present. The prairie and Symphoricarpos-sumach

associations are almost identical here and at Grant Hill and Engineer's Hill. The increased elevation at Government Hill results in a more xeric condition there.

Oak-Hickory Association.—The oak-hickory association is typical of the older upland woods of eastern Kansas. The most abundant trees are white oak, *Quercus alba*, L., white swamp oak, *Q. bicolor* Willd., shingle oak, *Q. imbricaria* Michx., blackjack oak, *Q. marilandica* Muench., pin oak, *Q. palus-*

PLATE 4.—The cracked dried mud of the sandbar is subsequently filled with sand and the scattered growth of the first vegetation occurs in these fillings.

tris Muench., bitternut hickory, *Carya cordiformis* (Wang) K. Koch, shagbark hickory, *Carya ovata* (Mill.) K. Koch, and pignut hickory, *Carya glabra* (Mill) Sqach. These trees are mostly of large size, one foot or more in D.B.H., and consequently form a dense forest canopy. In these woods the principal plants forming the understory of vegetation are may-apple, *Podophyllum peltatum* L., smooth Solomon's seal, *Polygonatum commutatum* (Schultes) Dietr., common violet, *Viola papilionacea* Pursh, woodland fern, *Woodsia obtusa* Torr., poison ivy, *Toxicodendron radicans* (L.) Kuntze, wood nettle, *Laportea canadensis* (L.) Gaud., and cleavers, *Galium aparina* L.

In some of the more open timber or where the old forest has died out, many elms, *Ulmus americana* L., buckeye, *Aesculus arguta* Buckl., and red bud, *Cercis canadensis* L., grow profusely. Other plants making up the understory of vegetation include bittersweet, *Celastrus scandens* L., persimmon tree, *Diospyros virginiana* L., wild columbine, *Aquilegia latiuscula* Greene, greenbrier, *Smilax hispida* Muhl., and buck brush, *Symphoricarpos orbiculatus* Muench. In the open woods and thickets, hemp, *Cannabis sativa* L., is common.

Black walnut, *Juglans nigra* L., is found throughout this region. Hard maple, *Acer nigrum* Michx., is confined entirely to a small area in the northern part of this region.

III. SHERMAN FIELD AND VICINITY

This community embraces the broad fan-shaped alluvial plain formed in the bend of the river to the east containing about 1446 acres. The area is almost level but increases slightly in elevation toward the river (775 feet) and then drops off rapidly to the low water level of 740 feet.

The eastern half of the area is mostly a subclimax deciduous forest of oak-hickory-pecan with a fringe about the exterior of the cottonwood-elm-sycamore association. In earlier times this forest covered much of the southern half of the area but on the western part was removed more than fifty years ago (Hunt & Lorence, *op. cit.*).

Cottonwood-Elm Association.—This association forms a rather well defined fringe, from 50 to 300 yards wide, around the oak-hickory association. Typically the growth is heavy; the trees range up to 70 feet tall and 6 feet D.B.H. The most abundant trees are American elm, *Ulmus americana* L., slippery elm, *Ulmus fulva* Michx., river poplar, *Populus deltoides* Marsh, soft maple, *Acer saccharium* L. and the sycamore, *Plantanus occidentalis* L.

In the southern part of this area the floor of the forest supports almost exclusively a society of the horsetails, *Equisetum arvense* L. and *E. fluviatile?* L.

Throughout most of the association the usual undershrubs are poison ivy, *Toxicodendron radicans* (L.) Kuntze, riverside grape, *Citis vulpina* L., northern plum grape, *V. labrusca?* L., Virginia creeper, *Psedera quinquefolia* (L.) Greene and greenbrier, *Smilax hispida* Muhl.

Oak-Hickory Association.—This association constitutes the interior of the

forested area consisting of a heavy growth of hardwod timber with a few scattered elms and cottonwoods. The forest is dense and the shade is almost complete. The common trees are shagbark hickory, *Carya ovata* (Mill) K. Koch, pignut hickory, *C. glabra* (Mill) Spach., pecan, *C. pecan* (Marsh) C. K. Schneid., black walnut, *Juglans nigra* L., and several species of oaks.

PLATE 5.—Oak-hickory association of Government Hill-North Hill vicinities. The upper photograph is of an old forested area; the trees have recently died out. The undergrowth is mainly ragweed, hemp, sunflowers, and buckbrush. This is a favored habitat of the woodchuck and spotted skunk. Pilot black-snakes and blue racers are numerous. The lower illustration is of a society of hard maple. Red-headed woodpeckers, bluejays and fox squirrels are common throughout this region.

In addition to the undershrubs of the cottonwood-elm association, numerous societies of cleavers, *Galium aparine* L., woodnettle, *Laportea canadensis* (L.) Gàud., and in a damp marshy place in the interior there is a pure stand of Gray's sedge, *Carex asa-grayi* Bailey. Scattered throughout are numerous jack-in-pulpits, *Arisaema triphyllum* (L.) Schott and smooth Solomon's seal, *Polygonatum commutatum* (Schultes) Dietr.

Sedge-Willow Association.—The sedge-willow association forms a broad ectone between the forest and mainland, extending across the peninsula from north to south.

This transitional zone has a greater number of habitats, both in quantity and kind, than any other association included in this survey. Conditions in the larger bushbrush sumach association closely approach those found in this type of a community.

In most of the area stabilization has not been approached and the change from the hydrophytic to the mesophytic condition is still in rapid progression.

The northern part of this alluvial plain is formed by numerous rapidly filling oxbow lakes and marshes; in most of these the water is replenished only during the very high water of early spring or by heavy rains. Throughout this region sandbars and embankments have become well covered with a thick growth of willows and cottonwoods, some of which are twenty to thirty feet tall.

The major portion of the remaining area consists of a mixed growth of trees, shrubs and weedy annuals. The more abundant trees, most of which are less than twenty feet in height, are river poplar, the willows, *Salix missouriensis* Bebb., and *S. interior* Rowlee, sycamore, *Plantanus occidentalis*, L., and tamarisk, *Tamarix gallica* L.

Most of the undergrowth in this type of cover consists of broad societies of horsetail, *Equisetum arvense* L., yellow cyperus, *Cyperus flavescens* L., shining cyperus, *C. rivularis* Kunth., nut grass, *C. rotundus?* L. and Wright's sedge, *Carex* sp.

Scattered among the clumps of bushes and trees are many patches of ragweed, *Ambrosia striata* Rydb., green foxtail, *Setaria viridis* (L.) Beauv., yellow bristle grass, *S. lutescens* Weigel, giant reed grass, *Phragmites communis* Trin., smartweed, *Persicaria lapathifolium* (L.) S. F. Gray, pink smartweed, *P. coccinea* (Muhl.) Greene, golden dock, *Rumex persicarioides* L., great water dock, *R. britannica* L., lamb's quarters, *Chenopodium album* L., Indian cup, *Silphium perfoliatum* L., Kansas sunflower, *Helianthus annuus* L., and hemp, *Cannabis sativa* L.

ANNOTATED LIST OF AMPHIBIANS

Included in this list are all specimens collected and those reported from this area. Species not collected but known to occur in the region are so indicated.

The two positive factors seemingly of prime importance for occurrence are suitable breeding places and places affording protection throughout dry

periods. Temporary rain pools permit many species to reproduce; cover is afforded by burrows, crevices under rocks and by surface debris. Breeding places and protection in dry periods may be present in only a small fraction of the total area of an association.

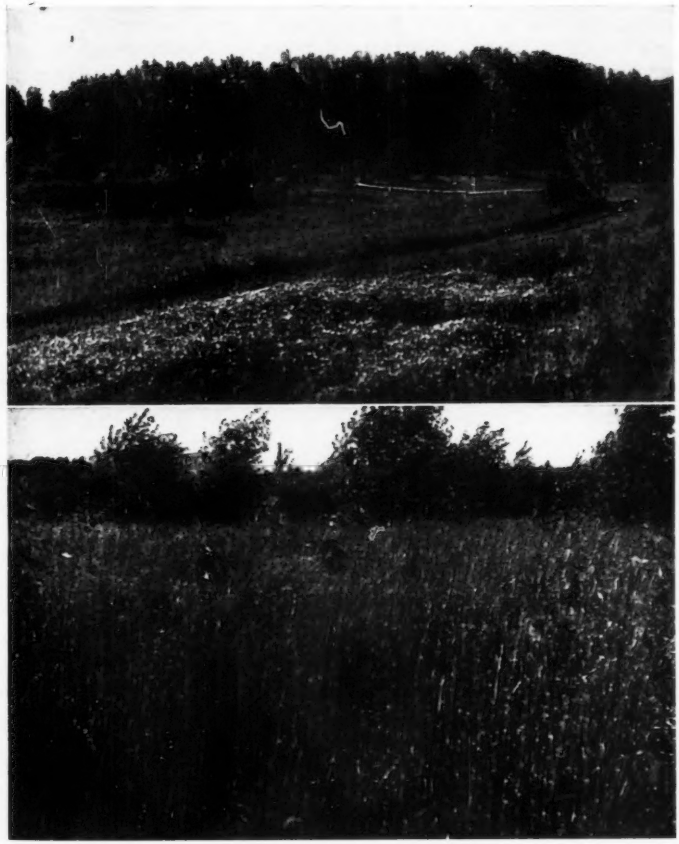


PLATE 6.—The upper photograph is a general view of the Sherman Field vicinity showing the sedge-willow and cottonwood-elm associations. Along the edge of this forest the population of *Peromyscus* was approximately eight per area. The lower view is of an extensive vicinity of horsetail extending from the sedge-willow association into the adjoining cottonwood-elm association. The cottontail rabbit is numerous throughout the associations.

Ambystoma maculatum (Shaw), Spotted Salamander.—Although this salamander has not been collected in this area its presence in the Kaw Valley Biotic district (Smith, 1934) indicates that it may yet be found.

Ambystoma tigrinum mavortium (Baird), Tiger Salamander.—Occasionally found in old water holes and especially in damp basements. No breeding areas were discovered.

Necturus maculosus maculosus (Rafinesque), Mudpuppy.—The mudpuppy was rarely found on the reservation. It is occasionally taken in the Missouri River and ponds near its banks. In some of the tanks on farms in this area it is common.

Bufo americanus americanus (Holbrook), American Toad.—American toads are more common in this region than Rocky Mountain toads, and were most numerous in the prairie and open woodlands. During the breeding season they are about twice as numerous as the Rocky Mountain form. They are generally distributed throughout the entire reservation. No males were heard calling or discovered in the Missouri River, although the species breeds freely in the small ponds adjacent to the river.

Bufo woodhousii woodhousii Girard, Woodhouse's Toad.—Although the American toad was more numerous than this species during the breeding season, the Woodhouse toad was more in evidence during rains that fell in the late summer. It was also more common in the heavily wooded oak-hickory association throughout the summer. During a rain in August seventeen of these toads were picked up in the vicinity of Grant Hill, while only seven specimens of the American toad were found; in the spring this ratio would be approximately reversed.

Acris crepitans Baird, Cricket Frog.—This is one of the most common frogs of the area, being found throughout in meadow and forest pools and along all the streams. Eggs were found only in the upper courses of the small streams and in the smaller ponds and temporary rain pools.

Pseudacris nigrita triseriata (Wied), Swamp Cricket Frog.—This frog is abundant in small ponds near streams and in the woods. Temporary ponds seem to be preferred as breeding places. In some regions this frog is more numerous than the common cricket frog. During April, 1939, it was heard constantly but soon disappeared and was not seen again until the rain of August 16, at which time it did not call.

Hyla crucifer Wied, Spring-Peeper.—The type specimen of this frog was obtained at "Cantonment Leavenworth, Kansas" in 1938; the species has not been found in this region since. It is hoped that some future collector will be able to secure additional specimens from this locality.

Hyla versicolor versicolor (Le Conte), Tree-toad.—The tree-toad seems to be rare in this region. Due to its secretive habits and almost perfect concealment it is usually encountered only by accident. Probably this frog is

more common than specimens would indicate. The specimens were taken from dead elm trees.

Rana catesbeiana Shaw, Bullfrog.—This species is a common inhabitant of the littoral association, although it is more numerous in the streams than in the quiet ponds. In June, 1939, more than one hundred and twenty were collected along Salt Creek. The tadpoles were usually found in the lower and more permanent parts of the tributaries. Not many of the larger bullfrogs escape the epicure in this part of the state.

Rana pipiens Schreber, Leopard Frog.—The spotted pond frog is numerous in most associations that offer the necessary moisture. Most of the individuals seen were at least half grown, although many that were younger were seined from the small creeks and ponds.

On August 16, 1939, while collecting during a rain, thirty-seven of these frogs were captured in a distance of one hundred yards along a bluff near the Missouri River.

While walking along the Missouri River in normal summer weather it was noted that these frogs hit the water with surprising regularity; upon counting the number of plopping frogs and the number of steps taken it was found that the frogs averaged one individual for each eleven steps. This procedure was followed on successive days along one mile of shoreline, and the average remained approximately the same. The frogs that were thus alarmed were usually at least half grown. After one had passed, they soon climbed from the river and took up their former positions on the bank, concealed under lumps of mud or debris.

Microhyla olivacea (Hallowell), Western Narrow-mouthed Frog.—In 1939 the results of extensive collecting indicated that this species was rare; only a few individuals had been found at widely separated places in the oak-hickory association in the vicinity of Government Hill-North Hill. In 1940 specimens were actually very numerous in the prairie association as well as in the open woodlands.

On one rainy night in August, fifteen specimens were collected and many more were seen. All those collected were very fat; twelve of these contained from sixty-five to eighty-five ants each. They were never heard calling at any season of the year.

ANNOTATED LIST OF REPTILES

This list includes specimens that have been collected in this area, those seen and identified with certainty as well as species whose general range includes this region.

Some kinds of reptiles occupy small ecological niches which allow protection for adults and young; however, their range for feeding may extend a considerable distance from this den. The absence of suitable niches would make it impossible for some species to maintain themselves in some areas.

Anolis carolinensis Voigt, Chameleon.—This lizard may be established along the Missouri River at Ft. Leavenworth and Leavenworth. In July,

1940, some boys brought me a lizard in a tin can, and said that they had killed fifteen others in the thickets along the bank of the Missouri River. This lizard proved to be *Anolis;* it was healthy and fat. I inquired about the neighborhood concerning these lizards and found that a family had been sent two dozen of them during the summer of 1938. They were kept until some time in August and then released not far from where they were found. It is a certainty that some of these lizards passed through the winter successfully. No other specimens were obtained.

Sceloporus undulatus hyacinthinus (Green), Southern Fence Lizard.—This lizard is rather rare; it was found along a rocky ledge in the oak-hickory association of the Government Hill vicinity.

Ophisaurus ventralis (L.), Glass-snake Lizard.—Several specimens of "glass-snake" were found by residents of Ft. Leavenworth. Some boys brought me one for identification which they had found in the cottonwood-elm association; they kept it for their own collection. Evidently this lizard is rare in this locality.

Cnemidophorus sexlineatus (L.), Six-lined Racerunner.—This was the most common lizard on the reservation. It was usually found in the old woodlands, especially about rotted logs and in rock ledges.

Leiolopisma laterale (Say), Brown Skink.—This lizard is rather rare. Only a few specimens were seen. These were near a limestone ledge in the cottonwood-elm association near Corral Creek.

Eumeces fasciatus (L), Five-lined Skink.—The five lined skinks are common throughout the hardwood forest of the higher areas, especially in the vicinity of Government Hill-North Hill.

Eumeces obsoletus (Baird and Girard), Sonoran Skink.—One of the few specimens found was in the prairie under a flat rock. The others were in the open woods near the edge of the forest.

Carphophis amoena vermis (Kennicott), Worm Snake.—This snake was common on the hillsides of the oak-hickory association in the vicinity of Government Hill-North Hill during 1939. Sometimes it was found under rocks in association with *Tantilla* and *Diadophis*. In 1940 only a few of these snakes were found. They were not found along the Missouri River bank where *Diadophis* was common.

Diadophis punctatus arnyi (Kennicott), Ring-necked Snake.—Ring-necked snakes are found mostly along clay banks or on hillsides where flat rocks abound. These areas are usually open woods or buckbrush-sumach formations. Along the clay banks they often inhabit fissures in the clay. In early spring, in damp weather, these snakes are observed numerously and are often found abroad during the day. During the hot dry weather of the summer they were not present in any of their usual haunts, but were estivating in their tunnels below the surface. A rain in August or September always brings them out for a few days.

In May, 1940, there were fourteen of these snakes on about one hundred yards of clay bank near the Missouri River. None of these snakes was ever found in the more mesophitic areas of the forest.

Heterodon contortrix (L), Puffing Adder.—No specimen of this snake was obtained but its range includes this region and it may occur in the area in limited numbers.

Coluber constrictor flaviventris (Say), Blue Racer.—This is one of the more common snakes of the reservation, especially in the vicinity of Government Hill-North Hill. In some places a half dozen individuals might be found within a radius of a hundred yards. A "nest" containing twenty-two eggs was found on the west slope of Miles Point. One of these eggs later hatched in the laboratory.

A few adults were seen in low trees; they are adept at escaping through the tree tops.

In the areas where these snakes and the pilot black-snake were most numerous the smaller rodents were rarely found.

Elaphe laeta laeta (Baird and Girard), Emory's Rat Snake.—Two young individuals of this rare species were found in 1939. One of these was taken from a willow tree.

Elaphe obsoleta obsoleta (Say), Pilot Black-snake.—The pilot black-snake was common in the old woodlands occupying the higher portions of the reservation. In the vicinity of North Hill three or four adults were found on almost every acre during the summer of 1940. It was there that the population of *Peromyscus* was so very low. This species was not found in the dense woods; the species seemed to prefer the open woods and thickets.

Pituophis sayi sayi (Schlegel), Bull-snake.—The bull-snake is rarely found in this area. No adults were found but several were reported killed by workmen about the post.

Lampropeltis calligaster (Harlan), Yellow-bellied King Snake.—These snakes were rather uncommon; one would expect them to be more numerous. A few were found on the prairie and in the more open woods in the vicinity of Government Hill.

Lampropeltis getulus holbrooki (Stejneger), Spotted King Snake.—The range of this subspecies includes this area but no specimens have been seen. Several boys have described snakes found on the reservation which undoubtedly were of this form.

Lampropeltis triangulum syspila (Cope), Red King Snake.—Red king snakes are rather rare, although personell of the Sanitary Corps reported that while cleaning up piles of stones and old brush they often killed these snakes. One was found under a large flat rock coiled among ring-necked snakes.

Natrix erythrogaster transversa (Hallowell), Blotched Water Snake.—One specimen was found dead on a sandbar in the Missouri River. The species is not nearly so common as *N. s. sipedon*.

Natrix sipedon sipedon (L.), Water Snake.—The water snake was common along Corral Creek, Salt Creek, the Missouri River and in some of the larger ponds on the north side of Sherman Field. Several were taken under rocks around a cool spring near Grant Hill.

Storeria dekayi texana Trapido, DeKay's Snake.—One individual was obtained in the open woods of the oak-hickory association. No other evidence of the species was found.

Haldea valeriae elegans (Kennicott), Brown Snake.—The range of this snake includes Ft. Leavenworth and it may be present.

Thamnophis radix (Baird and Girard), Plains Garter Snake.—A few plains garter snakes were found, but the species is not so common as the red-sided garter snake. Only one adult was seen, the rest being very young individuals.

Thamnophis sauritus proximus (Say), Western Ribbon Snake.—The western ribbon snake was found only in the prairie association. Records consist of three examples found dead on the road.

Thamnophis sirtalis parietalis (Say), Red-sided Garter Snake.—This is the most common garter snake. It generally inhabits the more mesophytic areas of the prairie; the moist clay bluffs of the buckbrush-sumach association and river and stream banks are its favorite haunts. Six specimens were collected near one spring along the Missouri River.

While I was observing birds in June, 1940, a pair of Bell's vireos started a commotion among some young elm trees; investigation revealed a large female garter-snake slowly making its way towards the vireos' nest which contained three young.

Tropidoclonion lineatum (Hallowell), Lined Snake.—Due to its rather secretive habits this species is seldom found in this area although it may be more abundant than present records would indicate. One snake was found dead on a road. Seven others were obtained in May, 1940, from approximately eighteen inches below the surface of the ground in a damp, rocky meadow near Corral Creek. On June 8, 1940, a large adult was obtained in the damp forest in the vicinity of North Hill. Earthworms were numerous in both of the last-mentioned situations.

Tantilla gracilis Baird and Girard, Slender Tantilla.—Several specimens were collected in the vicinity of Government Hill under flat rocks; most of them were in open woods. The species was rather common throughout this area in 1939 but fewer examples were seen in 1940. Sometimes it is found associated with *Carphophis*, rarely with the ring-necked snake.

Agkistrodon contortrix (L), Copperhead.—The copperhead is rare; the presence of large numbers of horses on the reservation has caused men who are interested in the horse to kill all poisonous snakes found. Of course almost every snake seen is immediately dispatched by those ignorant of its identity.

Sistrurus catenatus catenatus (Rafinesque), Massasauga.—The species is known from only one record, in Salt Creek Valley on the edge of the reservation, where a specimen was exposed by a crew building a road. In earlier days the settlers of this area reported that many of these rattlesnakes were turned up while plowing.

Crotalus horridus horridus (L), Timber Rattlesnake.—A large adult was picked up dead on a road in the oak-hickory association in the vicinity of Government Hill. Several other individuals were reported killed on the reservation. The species was found in the buckbush-sumach and cottonwood-elm associations along Corral Creek.

Chelydra serpentina (L), Common Snapping Turtle.—The snapping turtle is common in the Missouri River and the smaller streams. Several adults were found more than a hundred yards from water. In September, 1940, an adult was saved from the oak-hickory association in the vicinity of North Hill, at which time of the year the nearest water was more than four hundred yards away.

Very large specimens of this turtle are frequently killed along the Missouri River. On May 6, 1939, a large individual became entangled in the propeller of one of the river tugs and although badly mangled it took about an hour's work to free it from the shaft.

Terrapene ornata (Agassiz), Ornate Box Turtle.—The box turtle, although frequently encountered in late spring and early summer, must be considered rare. Many persons living in this locality for several years had never seen a specimen. In spring, box turtles were found in the oak-hickory forest in the vicinity of Government Hill. Later in the summer they were often found feeding on ripened mulberries which had fallen to the ground. These turtles are extremely fond of June bugs and crickets; these insects are preferred to other forms of food whenever there is a choice.

Graptemys pseudogeographica pseudogeographica (Gray), Mississippi Map Turtle.—This turtle was found mainly in backwaters from the Missouri River. It was rarely found in the small streams of the reservation drainage system.

Chrysemys picta bellii (Gray), Western Painted Turtle.—This turtle varied in its distribution; during 1939 few were seen but in June, 1940, it was common in the lower parts of the small streams. After a heavy rain few were seen during the entire ensuing summer. It is judged that they were swept out into the Missouri River from which they failed to return to the tributary streams.

Pseudemys scripta troostii (Holbrook), Troost's Turtle.—Troost's turtle was found in the shallow water of all the small streams; often several would be seen sitting on an old log in the river. They are not so numerous as the western painted turtle.

Amyda mutica (Le Sueur), Spineless Soft-shelled Turtle.—This species was found only in the old ponds left during flood stages of the Missouri River. There were mostly young individuals in these ponds, none being

larger than four inches across. Probably the species occurs in the Missouri River and the lower parts of its tributaries.

Amyda spinifera spinifera (Le Sueur), Spiny Soft-shelled Turtle.—Several turtles of this species were found along the Missouri River. Occasionally the species was found in the backwaters where stagnant ponds had been formed.

ANNOTATED LIST OF MAMMALS

The arrangement of the species and subspecies in general follows Miller (1924). Subspecies described subsequent to 1924 are included.

Didelphis virginiana virginiana Kerr, Opossum.—The opossum is a woodland species widely distributed in this area. Many are taken each year by hunters and trappers. A female picked up dead in April, 1940, on Grant Avenue, carried in her marsupium twelve very immature young. A half grown male was killed on March 13, 1940, in the cottonwood-elm forest in the vicinity of Sherman Field. Tracks of the opossum are commonly seen along the river and stream banks.

Scalopus aquaticus machrinoides Jackson, Eastern Mole.—The mole is a common fossorial inhabitant, probably ranging throughout the entire area from time to time. In some places in the vicinities of Government Hill and Grant Hill the ground is honeycombed by moles.

The vicinity of Engineer Hill consists of a golf course, bordered on the west for six hundred yards by the woodland of Cemetery Ridge. All moles are trapped as fast as they invade the golf course. From March 22, 1940, to June 16, 1940, 12 moles were trapped that had crossed the road into the golf course. Eight were females and four were males.

The autumnal rains seem to activate many moles in the prairie; these may have been active throughout the dry period but, if so, were confined to a greater depth or to the near-by moist woodland and ravine.

Moles tunnel extensively about patches of large weeds and brush, such as goldenrod, ragweed and buckbrush.

Several moles explored the new sandbars, tunneling out from the main bank of the river. Apparently these excursions are carried out in a hit or miss manner, the animal digging long "feelers" in different directions in search of food. Wherever a patch of sedge, grass, smartweed or young willows was reached the animal made many tunnels, suggesting that insects and their larva were numerous in these places. When a patch of young cottonwoods was entered the mole usually turned back after digging a short distance.

Blarina brevicauda brevicauda (Say), Short-tailed Shrew.—This shrew is not numerous in any association. One hundred traps in a quadrant in the sedge-willow association yielded a little more than one shrew to each two acres. Sign of this shrew was even scantier in the other associations where it was found.

Cryptotis parva (Say), Small Shrew.—Only one individual was found; it was in the cottonwood-elm association near Corral Creek.

Myotis keeni septentrionalis (Trouessart), Trouessart Bat.—Trouessart bat probably occurs, at least occasionally, in the Kaw Valley biotic district, for it occurs in the adjoining parts of Nebraska, Iowa and Missouri (Hibbard, 1933).

Myotis lucifugus lucifugus (LeConte), Little Brown Bat.—Only one specimen was taken in this area, but several times bats resembling this species in their manner of flight were observed feeding near the river and streams.

Eptesicus fuscus fuscus (Beauvois), Big Brown Bat.—The big brown bat is common during summer and hibernates locally in caves during the winter. Often several are seen flying over the river or woodlands, especially open woods. A few were seen feeding along the river bank late in the afternoon in October, 1939; at this time of the year the evenings were too cold to allow insects to be active except in the daytime.

Lasiurus cinereus cinereus (Beauvois), Hoary Bat.—The hoary bat was occasionally seen every summer. A female, with two half grown young, was obtained in an elm tree in July, 1939. Several were found dead after a violent storm in August. This bat is seldom seen over the Missouri River but was observed, on several occasions, feeding about lights near buildings.

Lasiurus borealis borealis (Müller), Red Bat.—Although only one red bat was obtained, several bats that were flying over the river and adjoining woodland were tentatively identified as belonging to this species.

Nycticeius humeralis (Rafinesque), Rafinesque Bat.—This bat is probably of occasional occurence in the Kaw Valley biotic district. It has been reported from the adjoining area in Missouri.

Euarctos americanus americanus (Pallas), Black Bear.—The black bear now is extinct in the area.

Procyon lotor hirtus Nelson and Goldman, Raccoon.—Tracks of the raccoon were frequently seen along all streams. Near the pools of water left by the recession of the river, tracks were always numerous as long as any fish remained in these pools.

A mother and half grown young raccoon were chased from a hollow oak tree near Grant Hill. This was a lone tree about fifty yards from the neighboring woodland. In the winter of 1939 a trapper near Corral Creek, who had just killed a racoon, said that he caught three or four raccoons on the reservation each winter.

Mustela frenata primulina Jackson, Long-tailed Weasel.—A female, caught in a rat trap, was kept captive at Ft. Leavenworth for over a year. Near the Missousi River, one was chased into a den. The den may have belonged to the weasel or to a Franklin ground squirrel which species was common at that place.

Mustela vison letifera Hollister, Mink.—The mink is not numerous but its tracks are evident, throughout most of the year, near the streams. The tracks of one were followed, after a new fall of snow, as they ran at right angles

to —and away from the Missouri River. The mink had gone out from the river about one hundred and fifty yards, apparently searching for food, and had then turned to the side for thirty or forty yards and proceeded back to the river. This hunting technic was repeated several times. These lines of tracks were roughly parallel.

Lutra canadensis lataxina (F. Cuvier), River Otter.—This species is thought to be extinct in the area studied.

Spilogale interrupta (Rafinesque), Spotted Skunk.—The spotted skunk is a common inhabitant of woodland and broken terrain about ledges, and railroad ballast. Evidence of this skunk was found in every association except the prairie. From the number of dens found occupied there could not be more than one *Spilogale* for every twenty or thirty acres.

Mephitis mephitis avia Bangs, Striped Skunk.—This skunk was rather rare; only two specimens were seen and about a half dozen dens were found on the reservation.

Vulpes fulva (Desmarest), Red Fox.—The red fox is rare although a few years ago it was rather common. A few foxes have been introduced in this region and have undoubtedly escaped in the wild. The last record of one killed at Ft. Leavenworth was in the early thirties.

Urocyon cinereoargenteus ocythous Bangs, Gray Fox.—The gray fox was reported as common in eastern Kansas in former days but it is now probably extinct throughout this area.

Canis latrans latrans Say, Coyote.—The coyote has been reported as common in the Missouri Valley region twenty to thirty years ago and for a time was considered almost extinct. However, in the last three years they have become common on the Military Reservation. Three were killed there in the fall of 1940; one of these was near the residential section of the post.

Canis lupus nubilus Say, Timber Wolf.—The timber wolf has long been only a legendary animal of this area.

Lynx rufus rufus (Schreber), Bobcat.—The bobcat disappeared from this area some years ago; however, its ecological niche may be occupied by the domestic cat which roams wild a good part of the year.

Marmota monax bunkeri Black, Woodchuck.—The woodchuck is common although its distribution is spotty. In the vicinity of Government Hill-North Hill it is most numerous; sight records and the number of occupied dens indicate a population of one or two animals to each 20 acres. Dens were in the prairie and buckbrush-sumach association. A few dens were in the woods but most of these were near clearings or in the more open timber.

Citellus franklini (Sabine), Franklin Spermophile.—A colony of a dozen or fewer of Franklin ground squirrels on the Missouri River bank, opposite Grant Hill, occupied the buckbrush-sumach association. After the sandbar was formed in the river near this locality they followed the moles in invading

it; often their burrows were merely elaborations of the moles' tunnels.

Citellus tridecemlineatus tridecemlineatus (Mitchell), Thirteen-lined Spermophile.—This species is usually common and occasionally numerous in the prairie association, and is found even in the mixed thickets. On the golf course the grass is kept short by mowing. There the population varies from one to two per acre. The numbers are kept in check by constant trapping as the spermophiles invade the more desirable portions of the greens. Probably many individuals migrate in from the surrounding prairie.

Preference was shown for the shallow valleys and ravines of upper One Mile Creek, where the *Citellus* took over the abandoned pocket gopher tunnels. During the spring and other wet seasons these tunnels were uninhabitable and the squirrels necessarily occupied the neighboring high ground.

The vicinity of Grant Hill—Pope Hill is prairie, thickets and mixed timber. Most of the prairie is heavily grazed and consequently overgrown by tall perennials such as goldenrod, yarrow, ragweed, narrow-leaved milkweed and sensitive briar. Here there are from one to two animals for each three or four acres. The spermophiles forage a good deal in the thickets of the transitional growth about the limits of the woodland. Most of the dens are twenty to fifty yards out in the prairie association.

One might expect the population to be greater in the habitat described above since food is more abundant there than in the vicinity of Engineer Hill. At Engineer Hill the terrain is more open and consequently a wider field of vision is afforded. Enemies appear to be equally abundant in both areas.

Tamias striatus griseus Mearns, Eastern Chipmunk.—Squirrel hunters may have contributed to the reduction in numbers of this species for it is shot because the hunters do not know what a chipmunk is. Only one animal was seen in this area; it was in the oak-hickory association in the vicinity of Sherman Field.

Sciurus carolinensis carolinensis Gmelin, Gray Squirrel.—This squirrel is found only in the woodlands in the vicinity of Sherman Field. It is not numerous, yet several are shot each year by squirrel hunters.

Sciurus niger rufiventer Geoffroy, Fox Squirrel.—The fox squirrel is numerous throughout the oak-hickory association. Since squirrel shooting has been allowed in the forests in the vicinity of Sherman Field, numbers have been considerably reduced. A low estimate of the number killed each year would be two hundred. The population of these squirrels has built up during the years to be in balance with the available food, mostly mast. In the past few years people have stripped the woods of all walnuts and pecans that they can find. During the fall of 1940 this was done so thoroughly that but little of these two forms of mast were left for the squirrels, and several times the squirrels were seen making trips into the weed patches, mainly ragweed, to collect seeds. Some of the squirrels traveled more than a hundred yards to gather food.

Counts of individuals and nests in the vicinity of Government Hill-North

Hill indicate a population of one squirrel for each two to three acres, but the distribution is not uniform.

Glaucomys volans volans (L), Eastern Flying Squirrel.—My one specimen was an animal killed by workmen while felling a tree.

Geomys bursarius majusculus Swenk, Pocket Gopher.—Pocket gophers are numerous in the vicinity of Government Hill-North Hill. In one area of mixed prairie they had so undermined the ground that it was difficult to walk over it because the tunnels caved in. Despite the abundance of pocket gophers, the vegetation was exceedingly rich and rank for the summit of a hill; in addition the soil was soft and loose. It was quite evident that under natural conditions, vegetation benefits greatly from the tillage accomplished by the pocket gopher.

Several specimens were obtained from different associations but not enough data was accumulated to allow for an estimate of the size of the population.

Castor canadensis missouriensis Bailey, Beaver.—There was a colony of beaver in the lower part of Salt Creek Valley a few years ago, but all traces of this colony have since disappeared. With the general increase in the population of the beaver it probably will again become established in this area. All the essentials for existence are here readily available.

Reithrodontomys montanus griseus Bailey, Gray Harvest Mouse.—No mouse of this species was found although the species occurs in the general region.

Reithrodontomys megalotis dychei Allen. Western Harvest Mouse.—Two specimens of this harvest mouse were obtained; one in a society of dock of the littoral association near the Missouri River, and the other was trapped in the oak-hickory association in the vicinity of Government Hill.

Peromyscus maniculatus bairdii (Hoy and Kennicott), Deer Mouse.—This mouse was not numerous in any association. The population, estimated from trap records, was not more than one animal per acre which for this species is an exceptionally low number. In many favorable habitats the house mouse was twice as numerous as the deer mouse. In similar areas where the house mouse was absent the population of *maniculatus* was more abundant. The deer mice were often found in an island of prairie isolated by surrounding timber. In one instance they must have migrated through about one hundred yards of cottonwood-elm forest in order to have established themselves on a sandbar recently deposited by the river. A pair, of breeding age, was collected here.

Peromyscus leucopus noveboracensis (Fischer), White-footed Mouse.—The size of population of the white-footed mouse in the different associations was estimated by trap-quadrants. These consisted of five parallel lines of twenty traps each spaced about fifty yards apart; the distance between traps in each line being ten paces. In some areas, especially at the edge of woods or along rocky ledges, a single line of traps was used. Calculation of density of population was based on the method described by Burt (1940).

The sedge-willow association of Sherman Field had an average population of four white-footed mice per acre during March, 1940. Along the edge of the cottonwood-elm association the population was eight per acre; the oak-hickory association averaged slightly more than three per acre. Here it was noted that the population fluctuated greatly, depending on the amount and kind of undergrowth present. In the brush and thickets along the bank of the Missouri River the population was three per acre. In the vicinity of Grant Hill-Engineer Hill the terrain is broken by many gullies and wooded ravines and the mouse ranges over much of the nearby prairie. The cottonwood-elm association along Corral Creek had a population of almost five per acre during March, 1939, but by November this had dropped to about 3 per acre.

Trapping records from the upper reaches of Corral Creek indicated a population of two per acre in November, 1940. In this locality it was noted that *Peromyscus leucopus* was trapped much farther out in the prairie than at any other place. The fringe of trees along the banks of Corral Creek was narrow here.

The vicinity of Government Hill-North Hill had the lowest population of these mice. During July, 1940, the woodland south of North Hill was trapped very extensively and the population appeared to be less than one individual for each two acres. In this formation the population of the pilot blacksnake and blue racer was one to two adults per acre.

During November and December, 1940, the Government Hill vicinity was trapped extensively and the population varied between one and two mice per acre.

Neotoma floridana osagensis Blair, Florida Woodrat.—The woodrat is not numerous in the area studied. Occasionally it came near garbage dumps and usually was trapped since no distinction was made between it and the common Norway rat. Florida woodrats occurred locally along the river bank and there were a few in the forested areas.

Synaptomys cooperi gossii (Coues), Cooper Lemming Mouse.—No evidence of this was observed, but it may have occurred in this locality in past years.

Microtus ochogaster ochogaster (Wagner), Prairie Vole.—This meadow mouse was numerous in the prairie and sedge-willow associations. Its preferred habitat was damp, rich, meadow land of blue grass, Johnson grass or sedge. The distribution was spotty; an acre or two would have many burrows and runways but an adjoining area would have only a few.

In the sedge-willow association the population averaged about one per acre over most of the area, but at a few stations the population was as high as four per acre in March, 1940.

In the prairie associations the populations varied from two per acre to nine per acre in November, 1940.

Pitymys nemoralis (Bailey), Pine Mouse.—Only a few pine mice were found in any association. Those trapped were taken in thickets, railroad ballast and on sandbars in the river.

Ondatra zibethicus cinnamominus (Hollister), Muskrat.—The muskrat is occasionally found along the Missouri River but is most numerous north of the sedge-willow association in the vicinity of Sherman Field.

Rattus norvegicus norvegicus (Erxleben), Norway Rat.—The Norway rat is common about dwellings and other buildings. Occasionally it is found in the woods near the garbage dumps. It is trapped and poisoned.

Mus musculus subsp.?, House Mouse.—The house mouse was quite common in some associations and often a mile or more distant from any habitation of man. Along Corral Creek, in the buckbrush-sumach association, the population varied from one to four per acre. In the prairie association the species was occasionally found in the same habitats as *Peromyscus maniculatus*.

Zapus hudsonius campestris Preble, Little Jumping Mouse.—The jumping mouse was not found in the area, but may occur in limited numbers.

Lepus californicus melanotis Mearns, Black-tailed Jack Rabbit.—A few years ago the black-tailed jack rabbit was rare in this region, but during the last year five animals were killed on the reservation.

Sylvilagus floridanus mearnsii (Allen), Florida Cottontail.—This species is common on the reservation. In the vicinity of Sherman Field the population averaged two to three per acre during June, 1940. In the winter the population is thought to be one per acre in this same place. In the woodland associations the population was somewhat less than in the sedge-willow association.

Cervus canadensis canadensis Erxleben, Wapiti.—Records of early explorers all mention the presence of this large game animal in the Missouri River Valley. It has long been extinct in the region of the reservation.

Odocoileus virginianus macrourus (Rafinesque), White-tailed Deer.—The white-tailed deer was once abundant in the woods of the reservation; this is evidenced by such reports as that of Lewis and Clark (see Hunt & Lorence, *op. cit.*).

In 1937 a captive white-tailed deer was brought to the reservation and is probably still there. The woodland associations of Ft. Leavenworth are judged to be capable of supporting a population of at least twelve deer without injurious results.

ANNOTATED LIST OF BIRDS

The taxonomic arrangement of the birds is in general according to the *Check-list of North American Birds* prepared by the American Ornithologists' Union, 1931 and subsequent revisions. Because most records are sight observations subspecific names are not used. The great mobility of the birds, the fact that many only pass through the area in migration and the further fact that many are resident for only a part of each year, combine to make it difficult to gain a complete knowledge of the avifauna in two seasons. The Missouri River Valley is a flyway for many migrant species of birds which

travel approximately the same routes year after year. For data on the arrival of the migratory forms reference can be made to Linsdale (1928). For the species or subspecies that are of probable occurrence in the ara the "Check-list of Kansas birds" by W. S. Long (1940) may be consulted.

Podilymbus podiceps (L.), Pied-billed Grebe.—The Pied-billed Grebe was observed twice on the Missouri River in spring, and in July, 1940, one was flushed from the sedge-willow association of Sherman Field.

Pelecanus erythrorhynchos Gmelin, White Pelican.—The White Pelican is a common migrant. In the spring of 1939 several small flocks fed for several days in the vicinity of Sherman Field and in September, 1940, two large flocks stopped at this feeding ground; one flock numbered three hundred and seventy five birds and the other about one hundred and eighty-two. One bird was shot from a small flock on November 22, 1940.

Phalacrocorax auritus (Lesson), Double-crested Cormorant.—The Double-crested Cormorants were shot by duck hunters on an oxbow lake in the vicinity of Sherman Field in 1939, and one was shot near the Missouri River in July, 1940. These birds are occasional migrants.

Ardea herodias (L), Great Blue Heron.—Three pairs of the Great Blue Heron remained in this vicinity during each of the two summers of my study. One pair entered and left the cottonwood-elm association on several occasions. The two other pairs were found in the sedge-willow association of Sherman Field. No nests were found. These birds spent considerable time on the sandbars in the Missouri River.

Casmerodius albus (L.), American Egret.—Only two birds were seen, both in September, 1940. They stopped for a short time on the bank of the Missouri River; after running about and doing some preening they continued their flight southward.

Florida caerulea (L.), Little Blue Heron.—The white immature form was seen both summers. Sometimes an individual would be on a sandbar every day for a week. Not more than five or six were seen in the two years and these were always single birds.

Butorides virescens (L.), Green Heron.—The Green Heron was common in this area; a pair nested in an oak tree near Merritt Lake in 1939. Two pairs nested in the cottonwood-elm association near Corral Creek and several were seen along the Missouri River and in the sedge-willow association in 1940.

Nycticorax nycticorax L., Black-crowned Night Heron.—A flock of about six of these herons was seen to alight on the Missouri River bank about dusk in October, 1940. No evidence of their roost or nesting site was found.

Botaurus lentiginosus (Montagu), American Bittern.—This bird was observed several times during migration; some fed along the river for several days. There was no evidence of their residing on the reservation.

Branta canadensis (L.), Canada Goose.—This species is present during

migration. In the spring of 1940 several thousand geese fed in the sedge-willow association for a couple of weeks. Many more were in the fields on the Missouri side of the valley. In the hunting season of 1940 several of these geese were killed on the Missouri River. Geese are far more numerous in the Missouri Valley in the spring than they are in the fall migration.

Branta bernicla (Linnaeus), Brant.—Hunters reported killing two brant in 1939, but I did not see the birds. Long (1940) reports brant as occuring in Leavenworth County. The species would be expected to migrate through this area, at least in spring.

Chen hyperborea (Pallas), Snow Goose.—The Snow Goose is common during migration; often flocks numbering several hundred to a thousand fed in fields in the Missouri River Valley.

Anas platyrhynchos L., Mallard.—A Mallard was reported nesting in the sedge-willow association during the spring of 1939, but it is believed this was a misidentification. The mallard is common during migrations but only brief stop-overs are the rule.

Anas rubripes Brewster, Black Duck.—Hunters reported shooting two of these ducks on a slough in the sedge-willow association in the fall of 1939.

Anas streperus L., Gadwall.—A few Gadwalls were seen, in migration, along the Missouri River. Hunters reported shooting a few in the hunting season.

Anas acuta L., Pintail.—Common during migration. In July, 1939, a brood of these ducks was seen in the sedge-willow association of Sherman Field. The brood was observed many times later in the summer as the birds flew across the Missouri River to feed in the fields. In the first part of August an adult male was with the flock.

Anas carolinensis Gmelin, Green-winged Teal.—The Green-winged Teal is common during migrations; many are shot each year by hunters in this area, especially along the Missouri River.

Anas discors L., Blue-winged Teal.—The Blue-winged Teal is not known to nest in this region although several birds have been reported in early fall. It is a common migrant.

Mareca americana (Gmelin), Baldpate.—Seen during migration; a small flock of these ducks was reported near the Missouri River in August. This may have been a brood.

Spatula clypeata (L.), Shoveller.—Common migrant, although it is never so numerous as some of the other ducks.

Aix sponsa (L.), Wood Duck.—The Wood Duck probably migrates regularly through this region. Four of these ducks spent most of September and part of October, 1940, on Merritt Lake. Possibly they occasionally nest in such isolated woodlands as the Sherman Field forest.

Aythya valisineria (Wilson), Canvasback.—Hunters report that during 1940 they saw many of these ducks. Two ducks, in a flock on the Missouri River, were identified as this species.

Aythya affinis (Eyton), Lesser Scaup Duck.—The Lesser Scaup is often shot by hunters along the Missouri River; evidently it is numerous during migrations.

Glaucionetta clangula L., Golden-eye.—The only Golden-eyes known in this locality were six birds observed on the Missouri River in the winter of 1939 and 1940. This is the only known instance of the wintering of this subspecies in Kansas (Brumwell, 1941).

Melanitta fusca (L.), White-winged Scoter.—Specimens from this region were reported by Long (1940); none was seen in the area by me.

Mergus merganser L., American Merganser.—Several pairs of the American Merganser were seen on the Missouri River, mostly in the spring and fall. From July to September, 1939, a pair was seen on the Missouri River near the sedge-willow association. Possibly they remained there the entire season.

Cathartes aura (L.), Turkey Vulture.—A pair of Turkey Vultures have nested on the reservation for several years; what becomes of their offspring is not known. These two vultures are a common sight over the reservation. In 1939 their nest was near an old stone quarry in the vicinity of Government Hill.

Accipiter velox (Wilson), Sharp-shinned Hawk.—Sportsmen occasionally shoot one of these hawks on the reservation, but usually they shoot many more broad-wings and marsh hawks. The Sharp-shinned Hawk is rare in this locality; one was shot, near Corral Creek in April 1940, that had just eaten an English Sparrow.

Accipiter cooperii (Bonaparte), Cooper's Hawk.—Although more common than the sharp-shin, the Cooper's Hawk was by no means numerous. One was shot in the cottonwood-elm association in 1939. Several times these beautiful hawks have been seen sitting on one of the side branches of a long snag; this bird has never been observed resting on the topmost branch of one of these dead trees. The nest of a Cooper's Hawk was reported destroyed in the Sherman Field forest in 1940.

Buteo jamaicensis (Gmelin), Red-tailed Hawk.—Two pairs of Red-tailed Hawks nested on the reservation, one in the oak-hickory association in the vicinity of North Hill and the other in the cottonwood-elm association in the vicinity of Sherman Field.

Buteo lineatus (Gmelin), Red-shouldered Hawk.—A pair of these hawks nested in a lone cottonwood near the upper part of Corral Creek. A few days after the young had hatched only one adult was ever seen about the nest. Each year in the fall migration many of these hawks are shot.

Buteo platypterus (Vieillot), Broad-winged Hawk.—The Broad-winged

Hawk nests as far west as the Missouri River Valley. A female was shot, and its nest destroyed, by a hunter, in June, 1940. One was shot in April; it contained a fully developed egg. If these hawks were not molested by man their number in this region would undoubtedly be much greater.

Buteo lagopus (Pontoppidan), Rough-legged Hawk.—A Rough-legged Hawk was shot by a hunter in the winter of 1940. This was the only one seen in the area.

Circus cyaneus (L.), Marsh Hawk.—The Marsh Hawk is the hawk most commonly seen on the reservation; the species is especially numerous during the spring and fall. No nesting records are known.

Pandion haliaetus (L.), Osprey.—The Osprey is rare in this region; it was seen near the Missouri River, but only twice.

Falco columbarius L., Pigeon Hawk.—Two Pigeon Hawks were flushed from the cottonwood-elm association near Corral Creek in the spring of 1939; they remained in this vicinity for two days and then disappeared.

Falco sparverius L., Sparrow Hawk.—The Sparrow Hawk is a familiar bird on the reservation; four pairs were known to nest in the cottonwood-elm and oak-hickory associations.

Colinus virginianus (L.), Eastern Bobwhite.—The Bobwhite has increased in numbers due to appropriate measures to preserve a large breeding stock.

The vicinity of Grant Hill supported at least fifteen birds during the summer of 1939, but by September poachers had reduced the number to three or four birds. The poachers use shot in a 22 caliber rifle and shot the quail while they were sitting, usually at mid-day.

Phasianus colchicus L., Ring-necked Pheasant.—Several flocks of these pheasants have been introduced on the reservation during the past two years. It is not known if they have bred there.

Meleagris gallopavo L., Turkey.—The Turkey is now extinct. It was reported as abundant in these forests when white men first arrived.

Fulica americana Gmelin, Coot.—The Coot is common in this region, especially along the Missouri River and on the north side of the sedge-willow association. Several pairs were observed near the river throughout the summer although no nests were found. Dead birds were found along the river in fall, evidently shot by hunters.

Charadrius semipalmatus Bonoparte, Semipalmated Plover.—Five of these plovers fed along a sand bar several times in September, 1940. They seemed to have found a favorable feeding ground for they would return to the same place after being flushed.

Charadrius vociferus (L.), Killdeer.—The Killdeer is a rare resident. One nested in the prairie association near Hill 881; two other pairs were seen in Salt Creek Valley. They are often seen in the period of migration.

Philohela minor (Gmelin), American Woodcock.—A lone woodcock was flushed in the oak-hickory association of North Hill in the fall of 1940. In this season it was reported as seen twice.

Actitis macularia (L.), Spotted Sandpiper.—A pair of these sandpipers nested near a sandbar opposite Corral Creek in 1939 and 1940. They raised three or four young each summer.

Tringa solitaria Wilson, Solitary Sandpiper.—This sandpiper was rather common for a few weeks during migration.

Totanus melanoleucus (Gmelin), Greater Yellow-legs.—Only one bird was observed; it was feeding along the bank of the Missouri River.

Totanus flavipes (Gmelin), Lesser Yellow-legs.—Only a few Lesser Yellow-legs have been seen and these were along the Missouri River in April, 1940.

Erolia melanotos (Vieillot), Pectoral Sandpiper.—Several flocks of this sandpiper have been flushed along the river sandbars in the migration season. They never remained in the vicinity for more than one to two weeks.

Erolia bairdii (Coues), Baird's Sandpiper.—A Baird's Sandpiper was shot near the Missouri River. This species was rarely seen.

Erolia minutilla (Vieillot), Least Sandpiper.—This little sandpiper was seen in the spring of 1940 along the Missouri River, but not in the fall migration.

Ereunetes pusillus (L.), Semipalmated Sandpiper.—Two birds were found dead on a sand bar in the Missouri River (spring, 1940); they had evidently been shot.

Larus argentatus Pontoppidan, Herring Gull.—The Herring Gull has been shot in Leavenworth in past years and probably occasionally migrates through this area.

Larus delawarensis Ord, Ring-billed Gull.—Until the spring of 1940 few gulls migrated through this region. In March, 1940, a few Ring-billed Gulls were seen, and by April they were seen in flocks of fifty and more. They came through this region again in the fall.

Larus pipixcan Wagler, Franklin's Gull.—On May 20, 1940, several flocks of Franklin's Gull flew northward over the river. Some of these flocks fed along the river and in neighboring fields but none remained long in this area.

Larus philadelphia (Ord), Bonaparte's Gull.—Several flocks of this gull migrated through this region in 1940.

Sterna forsteri Nuttall, Forster's Tern.—These terns, mixed with the Common Tern, were common for a few days in April, 1940.

Sterna hirundo (L.), Common Tern.—The common Tern migrated up the Missouri River for about two weeks during the spring of 1940. The

species was never in close flocks but instead in a loosely formed string all along the river; every few minutes one to three would fly past while farther to the south a few could be seen approaching.

Sterna antillarum (Lesson), Least Tern.—This tern was reported on the Missouri side of the river in 1940; it may occur at Ft. Leavenworth.

Chlidonias nigra (L.), Black Tern.—In May, 1940, the Black Terns were numerous for about two weeks. None was known to have stayed in this locality.

Zenaidura macroura (L.), Mourning Dove.—The nests of this dove are numerous, especially in the thickets and cottonwood-elm association, and it is found throughout the reservation. In one small patch of wild-crabapple four nests were found containing eggs (July, 1939); one week later three of the nests were empty and abandoned and in another week the other nest was also abandoned. On August 16 a dove was nesting in a vacated thrasher's nest in this ime thicket. During both 1939 and 1940 the doves were numerous; flocks or twenty to thirty were flushed from the prairies and thickets. They fed extensively on hemp and sensitive peas although many preferred the grasslands.

Coccyzus americanus (L.), Yellow-billed Cuckoo.—This common bird nested along the river bank in the cottonwood-elm association and in the thickets of the oak-hickory association. Its distribution was not uniform for there were large areas in which it was seldom seen. Several adults were seen to make many trips across the Missouri River and to return with food for the young; approximately a mile was involved in the round trip.

Coccyzus erythropthalmus (Wilson), Black-billed Cuckoo.—This cuckoo was heard several times in the forests but no specimen was obtained. Evidently the species is rare in this region.

Tyto alba Scopoli, Barn Owl.—The Barn Owl is common at this locality. Three specimens were brought to me by hunters who thought they had shot a rare and valuable bird. One roosted in the cottonwood-elm association; two others flew over the vicinity of Sherman Field.

Otus asio (L.), Eastern Screech Owl.—The screech owl is common, and often a nuisance to the residents of Ft. Leavenworth because the families of young birds make much noise at night. Several nesting pairs were observed in 1939 and 1940. All nests found were in the oak-hickory associations.

Bubo virginianus (Gmelin), Great Horned Owl.—Several specimens of this common bird were obtained and other individuals were seen in the woods. These owls frequently roost near a good hunting ground until their food supply is exhausted. This was observed in the case of a covey of quail and again in an area that had a considerable population of cottontails.

Strix varia Barton, Northern Barred Owl.—A Barred Owl was shot in the cottonwood-elm association; another was flushed from a large tree in the oak-hickory association of Sherman Field.

Asio wilsonianus (Lesson), Long-eared Owl.—Only one Long-eared Owl was seen; this was in 1939.

Asio flammeus (Pontoppidan), Short-eared Owl.—Three Short-eared Owls were shot in the winter of 1940 by hunters. Evidently this owl is a winter resident; but no evidence indicates that it breeds in this locality.

Antrostomus vociferus (Wilson), Whippoorwill.—The Whippoorwill is common during the summer; its notes are often heard in the evenings. This bird seemed to be more numerous during 1940 than during 1939.

Chordeiles minor (Forster), Nighthawk.—The Nighthawk was common throughout the reservation. Several pairs "nested" on the roofs of buildings. One of their favorite feeding grounds was over the Missouri River, where they were always seen in the evening twilight. In extremely hot weather the nighthawks would be flying by mid-afternoon.

In the spring and fall of 1940 three or four nighthawks, that were distinctly different from the eastern nighthawk in their manner of flight, were seen over the Missouri River. They may have been Sennett's Nighthawk, *Chordeiles minor sennetti* Coues rather than the resident race, *minor* (Forster), but no specimen was obtained.

Chaetura pelagica (L.), Chimney Swift.—The Chimney Swift was not so numerous in this region as in former years; however a few were seen each year. Probably these birds lacked suitable breeding places.

Archilochus colubris (L.), Ruby-throated Hummingbird.—The Ruby-throated Hummingbird is common in some habitats on the Post. About the dwellings, where there are large beds of flowers, it is common. Most nests were in the buckbrush-sumach associations.

Megaceryle alcyon (L.), Belted Kingfisher.—Two Belted Kingfishers were seen over the Missouri River. No nest was found on the reservation.

Colaptes auratus (L.), Yellow-shafted Flicker.—This flicker is a common resident, and is most conspicuous in the fall, when flocks fly from tree to tree in the forest. Several nests were in the cottonwood-elm association along Corral Creek. On July 18, 1939, a pair was feeding their brood of young which were able to fly well. The young sat in an almost vertical line on the trunk of a tree emitting discordant squawks, while the parent birds picked food from the bark and placed it in the mouths of the young.

Colaptes cafer (Gmelin), Red-shafted Flicker.—One was seen in September, 1940. The bird is uncommon in this region.

Ceophloeus pileatus (L.), Northern Pileated Woodpecker.—Two individuals of this rare woodpecker were seen. Residents of the Post reported nesting of the species but no nests were found by the author.

Centurus carolinus L., Red-bellied Woodpecker.—The Red-bellied Wood-

pecker is rare in this region, only a few being seen and these in the fall and spring.

Melanerpes erythrocephalus (L.), Red-headed Woodpecker.—The Red-headed Woodpecker is numerous, especially in the oak-hickory association. In October, 1940, several white-footed mice caught in traps were found with the brains eaten out. Several days later two of the red-headed woodpeckers were observed eating the brain of a mouse.

A family was observed while feeding after the young had grown large enough to fly well. All kept to the upper parts of the tall trees in contrast to the flickers which fed lower down. The young seemed to find their own food, but flew from tree to tree with the parents. If one of the young succeeded in finding a tasty morsel in a certain part of the tree all the others, in turn, would explore the same orea, some even giving the spot a few half-hearted pecks with their bills. The red-heads travel a good deal through the forest, and give the impression of being always on the move.

Sphyrapicus varius (L.), Yellow-bellied Sapsucker.—A few of these sapsuckers were seen on the reservation during migration.

Dryobates villosus (L.), Eastern Hairy Woodpecker.—The Hairy Woodpecker was common in the oak-hickory association, and occasionally was seen in other forest formations. Nests were found only in the vicinity of North Hill.

Dryobates pubescens (L.), Downy Woodpecker.—The Downy Woodpecker is numerous in autumn and spring; it is common throughout the summer in all the forested areas. During the cold weather of January and February, 1940, the bird was not seen.

Tyrannus tyrannus (L.), Kingbird.—The Kingbird is locally common but there are large areas where it is seldom if ever seen. Its most usual habitats were the edges of the forest or open woodland. It was often found along the Missouri River.

Tyrannus verticalis Say, Arkansas Kingbird.—Three Arkansas Kingbirds were seen at Ft. Leavenworth early in the spring of 1940. These probably were migrants.

Myiarchus crinitus (L.), Crested Flycatcher.—The Crested Flycatcher was rare. Three pairs nested in the oak-hickory association in the vicinity of Sherman Field. Two other pairs resided throughout the summer of 1940 in the oak-hickory forest in the vicinity of North Hill; no nests were found.

Sayornis phoebe (Latham), Eastern Phoebe.—The phoebe is a common resident. Its nests were scattered in both the cottonwood-elm and the oak-hickory association. More individuals and nests were seen in the latter association. One nest was in a lone oak tree in the vicinity of Grant Hill.

Empidonax virescens (Vieillot), Acadian Flycatcher.—The Acadian Flycatcher was rare; only one specimen was obtained.

Empidonax traillii (Audubon), Alder Flycatcher.—No nesting of this flycatcher was noted; the bird was seen only in the spring, when migration was under way.

Empidonax minimus (Baird and Baird), Least Flycatcher.—For two weeks in April, 1940, this flycatcher was numerous; as late as May they were occasionally seen.

Myiochanes virens (L.), Eastern Wood Pewee.—The pewee is common. In the depths of the oak-hickory forests it was seen on almost every day of summer.

Nuttalornis borealis (Swainson), Olive-sided Flycatcher.—A few flycatchers of this species were seen when spring migration was under way.

Octocoris alpestris L., Prairie Horned Lark.—The Horned Lark was occasionally seen in the prairie association and in Salt Creek Valley. It was more common in 1940 than in 1939.

Iridoprocne bicolor (Vieillot), Tree Swallow.—The Tree Swallow was common. All nests founl were near the Missouri River, most of them being in the cottonwood-elm associations. They fed over the river where they were often seen in flocks of other swallows.

Riparia riparia (L.), Bank Swallow.—Several Bank Swallows were seen over the Missouri River at various times in the summer months but their nests were not located. Many banks suitable for nesting sites were present in this region.

Stelgidopteryx ruficollis (Audubon), Rough-winged Swallow.—The Rough-winged Swallows were common summer residents; both mature and immature specimens were obtained. They fed over the Missouri River in the mixed flocks of other swallows.

Hirundo rustica L., Barn Swallow.—This swallow was rarely seen in 1939 but in 1940 it was common. The nests were in old buildings and under bridges.

Petrochelidon albifrons (Rafinesque), Cliff Swallow.—In spring and autumn, several were seen over the Missouri River. None was seen in summer.

Progne subis (L.), Purple Martin.—The Purple Martin nests locally, and numerously especially near Merritt Lake where nest-boxes have been erected. Scattered flocks of these birds feed over the Missouri River in almost every hour of the day in summer.

Cyanocitta cristata (L.), Blue Jay.—Blue Jays are present throughout the year at Ft. Leavenworth. They nest in the wooded sections, especially the oak-hickory association in the vicinity of Government Hill-North Hill. These noisy alarmists are especially evident in fall and winter. In October, 1940, several were observed in the vicinity of North Hill where redheaded wood-

peckers were numerous. A jay would fly to a branch, near the industrious redhead, uttering a loud squawk and strike his bill against the branch several times. After this performance was repeated two or three times the woodpecker would make a dash at the blue jay. The jay easily avoided his pursuer and would soon find another victim to annoy.

Pica pica (L.), American Magpie.—One bird, in April, 1940, remained in the neighborhood of a clump of osage orange for approximately a week.

Corvus brachyrhynchos Brehm, Crow.—Many crows were present in spring and fall but only a few at other times of year. In 1939 and 1940 only one pair nested and raised a family on the reservation, although several pairs that nested on the Missouri side of the river often fed on the Post. The resident population, including those from Missouri, did not exceed fifteen individuals.

Parus atricapillus L., Black-capped Chickadee.—This chickadee is numerous except during extremely cold weather. It is found in the forested areas and also the dense weed patches of the sedge-willow association.

Parus bicolor L., Tufted Titmouse.—The tufted Titmouse is as numerous as the preceding species and in winter and late autumn, a flock, consisting of the two kinds of birds, often feeds in the woods.

Sitta carolinensis Latham, White-breasted Nuthatch.—The nuthatch was rare. The few individuals seen were in the oak-hickory association.

Certhia familiaris L., Brown Creeper.—The Brown Creeper was a common resident throughout the year in 1940, except in the cold months of January and February.

Troglodytes aëdon Vieillot, Western House Wren.—The House Wren is common; several nests were in or around dwellings, but other nests were in the cottonwood-elm associations.

Thryothorus ludovicianus (Latham), Carolina Wren.—Several individuals were seen in the buckbrush-sumach association. A nest in a wild plum thicket was built on top of an abandoned brown thrasher's nest.

Mimus polyglottos (L.), Mockingbird.—In May, 1940, three pairs of mockingbirds built nests in the cottonwood-elm association near the Missouri River. All these nests apparently were completed but two weeks later they were abandoned and the adults were not seen again. No other nests or individuals were found.

Dumetella carolinensis (L.), Catbird.—Catbirds were numerous and prefer the stream valleys. Eight nests were found along a mile of the Missouri River; however, not all of this distance offered suitable nesting sites. The nests were invariably in dense thickets; in a plum thicket, that was not more than one hundred feet square, four nests were found but a week later they had been abandoned. A cowbird's egg was found in one nest.

Toxostoma rufum (L.), Brown Thrasher.—The thrasher was common throughout the forest formation. Many of the nests found were later

abandoned; one of these was used by a catbird and then in August a mourning dove was raising a family in the nest.

Turdus migratorius L., Eastern Robin.—Robins were numerous and nested throughout this region but were most common in the cottonwood-elm association and about dwellings. During September, 1939, flocks of seventy-five to one hundred robins fed in thickets and weed patches in the vicinity of Grant Hill. A few flocks were observed in the vicinity of Sherman Field. In the fall migration of 1940 robins were almost as numerous as in 1939. Robins were observed at Ft. Leavenworth in every month of the year.

Hylocichla mustelina (Gmelin), Wood Thrush.—The Wood Thrush is almost rare in this region; only a few pairs were seen. The secretive habits of this thrush which lives in the forest thickets contribute to its inconspicuousness.

Hylocichla ustulata (Nuttal), Olive-backed Thrush.—A few individuals of this species were seen in May, 1940.

Sialis sialis (L.), Bluebird.—In early spring there were many migrating bluebirds along the Missouri River and in the sedge-willow association. None was observed nesting.

Polioptila caerulea (L.), Blue-gray Gnatcatcher.—This species was common and present through most of the year in the forest formations.

Regulus satrapa Lichtenstein, Golden-crowned Kinglet.—A few of these kinglets were seen in the spring and fall migrations, mostly in the buckbrush-sumach associations.

Regulus calendula (L.), Eastern Ruby-crowned Kinglet.—In the fall and early winter a few individuals were seen. None was observed in the colder part of the winter.

Bombycilla cedrorum Vieillot, Cedar Waxwing.—Reported as seen about dwellings at Ft. Leavenworth; none was seen by the author.

Lanius ludovicianus L., Migrant Shrike.—This shrike was common. It usually nested in the thickets at the edges of the woods.

Sturnus vulgaris L., Starling.—Starlings were first seen in the fall of 1939; they were in flocks of between fifty and seventy-five birds. In the early spring they dispersed to the surrounding forests. Old woodpecker holes were commonly used as nesting sites. The redheaded woodpecker arrived later in the spring and several of the starlings were evicted from their nests. Although there is no competition for food between these two birds, there appears to be intensive competition for nest sites. Several starlings that were able to continue their nesting in the woodpecker's range did not raise any young to maturity, possibly because the redhead's taste for flesh led him to destroy the young. In 1940 starlings were occasionally seen but were no longer common.

Vireo bellii Audubon, Bell's Vireo.—This vireo may be the most numerous small bird on the reservation. It was exceptionally numerous near the Mis-

souri River. Most nests were near the ground in young elm trees. As noted above in the account of the red-sided gartersnake, this bird may be the prey of that snake. Three nests were found to be parasitized by the cowbird; the cowbird eggs were removed from two of these nests and the third nest was not disturbed. The young cowbird soon occupied the entire nest; the young vireos were pushed "overboard" and the two adult vireos were left to feed their giant "offspring."

Vireo olivaceus (L.), Red-eyed Vireo.—The red-eyed vireo is common in the oak-hickory association in the vicinity of Sherman Field. A few stray individuals were seen in other associations.

Vireo gilvus (Vieillot), Warbling Vireo.—Only one pair of these rare vireos was seen; they nested at the edge of the cottonwood-elm association near Corral Creek.

Mniotilta varia (L.), Black and White Warbler.—Several individuals were seen in the spring migration. Three pairs nested on the reservation; one nest was near a spring in the cottonwood-elm association and the other two were in the dense forest of the oak-hickory association in the vicinity of Sherman Field.

Protonotaria citrea (Boddaert), Prothonotary Warbler.—This warbler could be classed as common on the basis of the number of pairs seen, but only three pairs were observed nesting. Each raised young; these were all in a heavily wooded ravine in the vicinity of North Hill. Eight pairs were seen in 1939, but only two pairs were seen in 1940.

Vermivora peregrina (Wilson), Tennessee Warbler.—Only a few of these rare warblers were seen, and those in spring only.

Dendroica petechia (L.), Yellow Warbler.—The Yellow Warbler was common in approximately the same associations inhabited by Bell's vireo. It nested in the taller trees and bushes near the Missouri River and Corral Creek.

Dendroica coronata (L.), Myrtle Warbler.—Three warblers seen in the spring of 1940 were tenatively identified as belonging to this species.

Seiurus aurocapillus (L.), Oven-bird.—The Oven-bird was occasionally seen in the spring migration. In June, 1939, a pair nested in the cottonwood-elm association near a spring; black and white warblers nested in the same habitat. In 1940 a pair nested in the oak-hickory association in the vicinity of Sherman Field.

Oporornis formosus (Wilson), Kentucky Warbler.—This species was common in suitable habitats. In a heavily wooded ravine in the vicinity of North Hill three pairs nested in 1940. A few other pairs were found in the other forest formations.

Geothlypis trichas (L.), Northern Yellowthroat.—Three yellowthroats were seen, one in 1939 and the other two in the spring of 1940. No nest was observed.

Icteria virens (L.), Yellow-breasted Chat.—The yellow-breasted chat was rather common in the forested areas. No nest was observed but adults were seen carrying food into the forest.

Setophaga ruticilla (L.), Redstart.—The Redstart is one of the very early spring arrivals. It was observed nesting in the cottonwood-elm association near Corral Creek and in the oak-hickory association in the vicinity of North Hill and Sherman Field.

Passer domesticus (L.), English Sparrow.—The English sparrow is still numerous in this region, possibly because the reservation has many horses, the feces of which provide food for this sparrow. No nests were found in trees; nesting sites about dwellings seem to be preferred.

Sturnella magna (L.), Eastern Meadowlark.—A pair of Eastern Meadowlarks, identified by their song, nested in the prairie association in the vicinity of Grant Hill. More Eastern Meadowlarks may have been present but this is the only pair of which the song was heard.

Sturnella neglecta Audubon, Western Meadowlark.—The species was common, although most numerous during the fall and early spring. It was found nesting in Salt Creek Valley and near Hill 881.

Xanthocephalus xanthocephalus (Bonaparte), Yellow-headed Blackbird.—Two individuals were seen in the willows along the Missouri River in the spring migration of 1939. No nest was observed.

Agelaius phoeniceus (L.) Red-wing.—The species was numerous in the sedge-willow associations. The population of the blackbirds was determined by direct observation. During August these birds are still in their family groups or one or two families have joined to form a small flock. In the evening, before sundown, they gather in the tree-tops; as dusk approaches the flocks fly to their roosts in the dense willows along the Missouri River. The author stationed himself on a hilltop and by using a pair of field glasses counted the birds as the flocks went to roost. In 1939 fifteen family groups were counted on successive evenings. The number in each group varied from five to seven birds. In 1940 there were seventeen groups with from three to nine individuals in each or one hundred and three blackbirds in all.

The breeding birds are presumed to be of the nominate race, the Eastern Red-wing. Several specimens collected in migration closely resembled the Giant Red-wing, *arctolegus* Oberholser, except in measurements of the bill. The Thick-billed Red-wing, *fortis* Ridgway, was numerous during spring migration. A pair was shot in the sedge-willow association in May; the female contained an almost completely formed egg. A male was collected in this region in July. Indications are that this subspecies is a rare resident in this region.

Icterus spurius (L.), Orchard Oriole.—This oriole is common and occurs throughout the forest formations.

Icterus galbula (L.), Baltimore Oriole.—The Baltimore oriole has a population about equal to that of the orchard oriole.

Euphagus carolinus (Müller), Rusty Blackbird.—A specimen was obtained in the sedge-willow association in March, 1940; it was in very poor condition. The species was rare.

Quiscalus versicolor (Vieillot), Bronzed Grackle.—The grackle is numerous during the fall and spring migrations. Breeding records in this region indicate that it is a common summer resident although widely scattered in distribution in the sedge-willow association.

Molothrus ater (Boddaert), Cowbird.—The species is common. In the fall and spring it was usually found associated with blackbirds and grackles. During the summer the adults are scattered throughout the region. Kinds of birds in the nests of which the cowbird's eggs were laid included Bell's Vireo, Catbird, Robin, Mourning Dove, Blackbird and Brown Thrasher. None of the eggs laid in the Mourning Dove's "nest" was known to hatch.

Piranga olivacea (Gmelin), Scarlet Tanager.—A few examples of this rare tanager were seen; one pair nested in the area in 1939 and 1940.

Piranga rubra (L.), Summer Tanager.—Only a few Summer Tanagers were seen in the forested regions.

Richmondena cardinalis (L.), Cardinal.—Common in the thickets of the woodland formations, the cardinal is present throughout the year.

Pheucticus ludovicianus (L.), Rose-breasted Grosbeak.—The species was common in the cottonwood-elm association. Few were seen in 1939, but in the summer of 1940 many nested in the tall trees near the Missouri River. The adults were obtaining food, for their young, in the fields on the Missouri side of the river.

Passerina cyanea (L.), Indigo Bunting.—The Indigo Bunting was commonly found in the forested areas; usually the males were perched on a prominent dead tree.

Spiza americana (Gmelin), Dickcissel.—This species was common throughout the prairie association and in the sedge-willow association.

Spinus tristus (L.), Goldfinch.—This bird was common and nested in the cottonwood-elm association.

Pipilo erythrophthalmus (L.), Red-eyed Towhee.—This bird was a rather uncommon resident; nevertheless it was common during the fall and spring in the forests and thickets.

Passerulus sandwichensis (Gmelin), Savanna Sparrow.—A few of these sparrows were seen and a specimen was obtained in the sedge-willow association.

Ammodramus savannarum (Gmelin), Grasshopper Sparrow.—A few Grasshopper Sparrows were seen in the prairie association.

Passerherbulus caudacutus (Latham), Leconte's Sparrow.—Several of these sparrows were seen in the spring and fall; none was seen in winter.

Pooecetes gramineus (Gmelin), Vesper Sparrow.—The species was common in the spring of 1940 in the thickets along the Missouri River.

Chondestes grammacus (Say), Lark Sparrow.—Only a few of these sparrows were seen in Salt Creek Valley.

Junco hyemalis (L.), Slate-colored Junco.—The junco was numerous during the winter of 1939 and during the spring and fall of 1940 but was entirely absent during the cold weather of January and February, 1940.

Spizella arborea (Wilson), Tree Sparrow.—This sparrow was numerous in the winter. A few specimens were taken in the summer but the species is not known to nest in this area. Most of the Tree Sparrows are referable to the Eastern Race, *arborea* (Wilson).

A few specimens taken were assigned to the western sub-species, *ochracea* Brewster; they were shot in thickets along the Missouri River.

Spizella passerina (Bechstein), Chipping Sparrow.—The species was common, although only a few are known to nest in this area.

Spizella pusilla (Wilson), Field Sparrow.—One nest was found near Grant Hill, and two others in Salt Creek Valley.

Zonotrichia querula (Nuttall), Harris's Sparrow.—This is one of the most numerous sparrows during the fall and winter. It is usually found in the thickets and in the weed patches of the sedge-willow association.

Passerella iliaca (Merrem), Fox Sparrow.—Although numerous during the spring migration the species was not observed in the fall or winter. Flocks of this sparrow were seen in the sedge-willow association and other thicket growths along the Missouri River.

Melospiza georgiana (Latham), Swamp Sparrow.—Sparrows of this species were common in the thickets along the Missouri River and in the sedge-willow association.

Melospiza melodia (Wilson), Song Sparrow.—The species was common throughout the area but especially in the sedge-willow and symphoricarpos-sumach associations.

ACKNOWLEDGMENTS

I am indebted to Professor Henry H. Lane for supervision of my work. Much valuable assistance was rendered by Professors A. Byron Leonard, Edward H. Taylor, Claude W. Hibbard and Worthy H. Horr in the identifications of specimens. I am indebted also to Mr. Charles D. Bunker, for the use of the resources of the Museum and for many helpful suggestions and criticisms. The Commandant, Fort Leavenworth, Kansas, kindly granted permission for this survey of the Military Reservation to be made. I am indebted to him and the members of his Command for many courtesies and much valuable assistance in locating and collecting specimens.

CONCLUSIONS

The Fort Leavenworth Military Reservation is situated on the west bank of the Missouri River near the eastern limit of the Missouri Valley Biotic District of Kansas.

The 4042 acres studied were divided into three main areas on the basis of physiographic features and these in turn were subdivided into associations according to the controlling flora. These associations were, Prairie Association, *Symphoricarpos* (buckbrush)-Sumach Association, Cottonwood-Elm Association, Oak-Hickory Association, Sedge-Willow Association and Littoral Association.

The distribution of the reptiles and amphibians is more dependent upon temperature and humidity than are the distributions of the other land vertebrates of this region. Cover and food are of greater importance in determining the distribution of the mammals.

The birds are readily divided into forest, prairie or littoral forms although many of them may breed in one association and feed almost exclusively in another.

Most species of birds nested throughout the forest formation, the controlling factors seeming to be suitable cover, light, temperature, and elevation for nesting sites.

The greater number of forms studied are similar to the forms which inhabit the Central Hardwood forest and tall and mid-grass prairies.

REFERENCES

AMERICAN ORNITHOLOGIST'S UNION 1931—Check-list of North American Birds. 4th ed. Lancaster, Pa. 526 pp.

BLAIR, W. F. & HUBBELL, T. H. 1938—The biotic districts of Oklahoma. Amer. Midl. Nat. 20: 425-454.

BRITTON, N. L. & BROWN, A. 1923—An illustrated flora of the northern United States and Canada. 2nd ed. Chas. Scrib. Sons. N. Y. Vol. I, pp. 1-677; Vol. II, pp. 1-731; Vol. III, pp. 1-560; 4666 figs. in text.

BRUMWELL, M. J. 1941—American Golden-eye a winter resident of Kansas. Auk 58: 94.

BURT, W. H. 1940—Territorial behavior and populations of some small mammals in southern Michigan. Misc. Pub. Mus. Zool., Univ. Mich. 45: 7-58, 2 pls., 8 figs., 12 tabs.

HINDS, H. & GREEN, F. C. 1917—Leavenworth-Smithville Folio (Missouri-Kansas) no. 206. *In* Geologic Atlas of U. S., U. S. G. S., Dept. Int., Washington, D. C., pp. 1-15, 10 pls., 10 figs., 4 maps.

HONEYCUTT, F. E. 1940—Report of the secretary, Leavenworth County Fish and Game Development Association. Sept. (MS).

HUNT, COL. E. & LORENCE, CAPT. W. E. 1937—History of Fort Leavenworth, 1827-1937, 2nd ed. The Command and General Staff School Press, Ft. Leavenworth, Kans. 301 pp., illus., pls. (1 fold.), 3 diagr. (fold.).

LEOPOLD, A. 1937—Game Management. Chas. Scrib. Sons. N. Y. 481 pp., front., 35 figs., 53 tabs.

LINSDALE, J. M. 1927—Amphibians and reptiles of Doniphan County, Kansas. Copeia, 164: 75-81.

———1928a—Mammals of a small area along the Missouri River. Jour. Mamm., 9: 140-146.

———1928b—Relations between plants and birds in the Missouri River region. Univ. Kans. Sci. Bull., 18: 499-515.

———1928c—Birds of a limited area in eastern Kansas. Univ. Kans. Sci. Bull., 18: 517-626.

———1933—The nesting season of birds in Doniphan County, Kansas. Condor, 35: 151-160.

LONG, W. S. 1940—Check-list of Kansas birds. Trans. Kans. Acad. Sci., 43: 433-456.

MCCOLLOCH, J. W. 1926—*In*, Shelford, Victor E., ed., 1926, Naturalist's guide to the Americas, Williams & Wilkins Co., Baltimore, Md. 761 pp., col. front., 15 figs. (part double).

MERRIAM, C. H.; BAILEY, V.; NELSON, E. W.; PREELE, E. A. 1910—Fourth provisional zone map of North America. *In* American Ornithologist's Union Check-list, 3rd ed. Lancaster, Pa., col. front.

MILLER, G. S. 1924—List of North American recent mammals. Smiths. Inst. Bull., 128: 1-673.

RYDBERG, PER AXEL. 1932—Flora of the prairies and plains of central North America. N. Y. Bot. Garden, N. Y. 969 pp., 600 figs.

SMITH, HOBART M. 1934—The amphibians of Kansas. Amer. Midl. Nat., 15: 377-528, 20 pls., 24 maps.

VAN DERSAL, WM. 1938—Native Woody Plants of the United States. U. S. Dept. Agr. Misc. Pub. 303, pp. 1-362, 44 pls., 3 figs.

WEAVER, J. E. & CLEMENTS, F. E. 1938—Plant ecology. McGraw-Hill, N. Y. 601 pp., front., 271 figs., 12 tabs.

The Biology of Leiolopisma laterale (Say)

Thomas Howard Lewis

U. S. Naval Unit, White Sands Proving Ground, Las Cruces, New Mexico

Leiolopisma laterale is a common North American lizard, but because of its small size and secretive habits its life history is imperfectly known. The species is found over most of the eastern and southern United States from the Atlantic coast to central Kansas and Oklahoma, and from southern New York to Florida and the gulf coast of Texas. The genus similarly enjoys a wide distribution, Asia, Australia, North and Central America (Smith 1946).

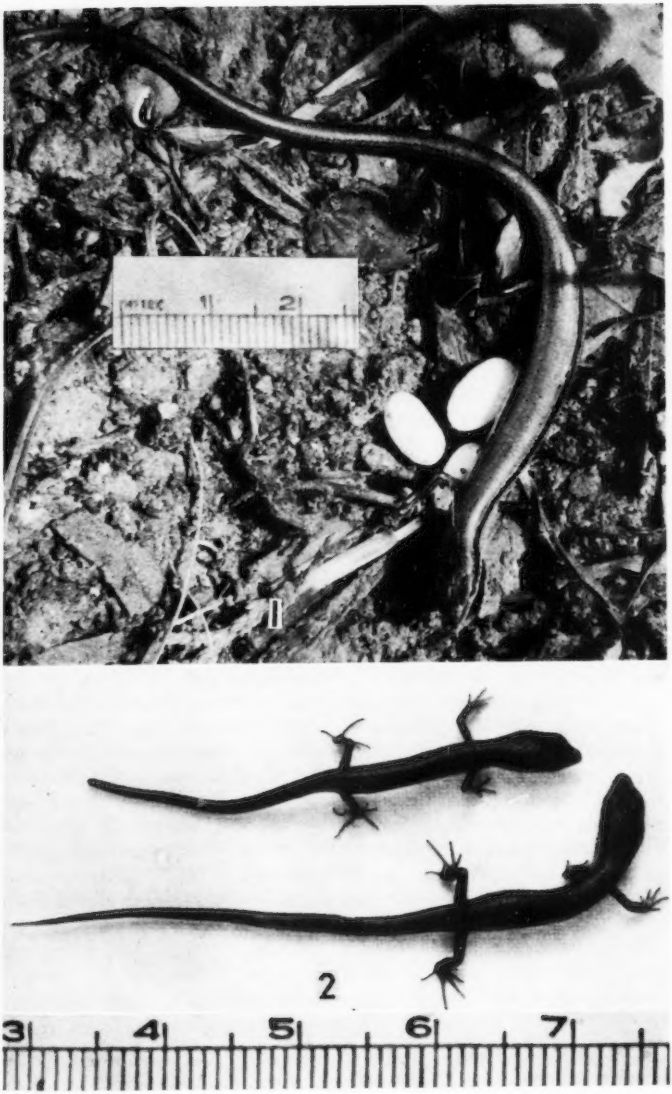
In order to review and enlarge upon previous observations, a thriving colony of *Leiolopisma laterale* within the city limits of Houston, Texas, was studied through 1946-1947. In addition, less extensive notes were made at irregular times previous in North Carolina, Arkansas, Oklahoma, and Louisiana. The Texas population, which is the subject of this report, occupied a wooded area approximately one-half mile square. Field observations were made several times a week, and at varying hours, under varied weather conditions, and in various habitats. The lizards were disturbed as little as possible, notes being made with the aid of a field glass. One quarter of the area was set aside for sampling. This square yielded specimens for dissection, and for maintaining a series of laboratory cages. Specimens were taken at various times throughout the year, and when no longer useful were preserved or released at distant points. Thanks are due to Mr. Bruce Taylor for assistance with the field work, and to Mr. Thomas E. Pulley, University of Houston, who undertook the tedious work of identifying insect fragments in stomach contents.

Description

The individuals of *Leiolopisma* collected in Houston correspond in general to the published descriptions of the species. The following listed characters were drawn from specimens typical of the adult population; — a small brown lizard (average weight 1.28 gm.), with body slender, cylindroid, and elongate (41-54 mm.); tail long (75-90 mm.) and slender; limbs very small and weak; toes elongate and clawed; scales mostly small, smooth, imbricated; scales around mid-body about 30, dorsal scales about 71; head up to 10 mm. in length; palpebral disc present; lateral color dark brown peppered with black; dorsal stripe wide, varying from copper to tan or brown; ventral color not as described in other populations (white), being instead greenish to bright yellow; the dorsum of the head and tail match the dorsal stripe in color.

Ecology

Leiolopisma laterale occupies areas with a thick ground cover of grasses or dead leaves, either in or on the edges of fairly dense stands of trees. Individuals of this species do not venture far onto open ground, or favor exposed posi-



Figs. 1, 2. *Leiolopisme laterale* (Say).—1. Adult female with eggs. About one inch of earth and leaf mold covered the nest; 2. Two newly hatched young, one of which has already been mutilated by a larger lizard.

tions. In the Austro-riparian of Houston (altitude 40 feet, annual rainfall 45 inches, average summer temperature 80-90° F., average winter temperature 50-60° F., soil a sandy clay of southern prairie type) the trees are mostly oaks heavily hung with Spanish moss, pines, hickory, occasional magnolias and palmettos. Beneath them is an undergrowth of smilax and poison ivy, and a thick carpet of rotting leaves and twigs. The soil is damp, with a water table but a few inches below the surface. Open ponds and ditches are periodically filled by the frequent heavy rains.

In North Carolina the brown skinks were almost indicators of beech forests. In New Orleans they were found in backyard gardens or beneath seed boxes or lumber in greenhouses and plant nurseries.

Leiolopisma is an unsocial lizard. Individuals caged together eventually fight. In the field they are not found in any sort of group, although no observations are yet available on courtship and mating. Some territory dominance probably exists since individuals distinctive enough to be recognized were observed many times in the same area. One gravid female whose residence was a particular crevasse beneath a pile of rotting shingles was seen with field glasses almost daily for several months.

GENERAL HABITS

Periods of activity.—Hibernation of *Leiolopisma laterale* in Houston is irregular. Warm sunny days occasionally occur throughout the winter, and on these days the lizards became active in the warmer part of the afternoon. *Leiolopisma* could always be collected in less pleasant weather by overturning stone and logs, and was a good source of live food during the winter for other laboratory animals. During the warm months a pronounced diurnal variation in activity was observed. *Leiolopisma* could not be collected at dawn. By mid-morning when the temperature had increased, lizard activity reached a peak, which soon fell almost to a complete quiescent base line during the hottest part of the day. About four o'clock in mid-summer, lizards again emerged, and between this hour and dusk both adults and juveniles were most active. Collecting in summer was always best in a two-hour interval before dusk, became poorer with twilight, and with frank darkness the lizards were all under cover. Extensive efforts to find lizards above ground at night were fruitless. In early spring and late fall the two periods of activity were fused, and corresponded to the warmest part of the day. As summer waxed the two active periods grew further apart, and as summed waned they drew nearer.

In the laboratory, lizards observed darkness as a signal for burying themselves in the soil or grass clumps of the cages. They gradually learned to become active at night when feeding was consistently delayed to the late hours of the evening.

Collecting.—*Leiolopisma* is difficult to collect. The presence of a specimen may first be known by a slight rustling in the forest floor, followed by silence. If seen, the lizard is moving rapidly toward cover, and once hidden in vegetable detritus or soft humus seems literally to have disappeared. The collector

must depend on a rapid hand to pin down the lizard or to seize it plus dirt, twigs and grass stems. An immunity to poison ivy is useful. Trapping or shooting is not practicable.

Locomotion.—The limbs of *Leiolopisma* are short and weak. They are of distinctly secondary importance in locomotion. The anterior and posterior pair of legs are often held back against the sides of the body while the lizard progresses by a violent lateral undulatory thrashing motion of the body and tail. In humus and at grass roots this type of progression is quite effective, and probably represents a tendency toward a limbless fossorial life. When moving slowly through tangled grass or twigs the feet are used as climbing aids.

Fighting.—In the presence of small snakes or other lizards (*Sceloporus* and *Anoles*) behavior similar to that in frightened *Gerrhonotus* is seen The lizard when unable to escape, as in an open laboratory cage, adopts a pattern of bluffing. The neck is flexed very sharply in the direction of the threatening presence, respirations are altered to a marked hyperpnea and polypnea, the tail is lashed in a violent and irregular manner. This behavior pattern is interrupted by periods of wild, unadaptive, running and climbing motions. *Leiolopisma laterale* in the presence of other members of the species resorts to fighting, mutilation, and cannibalism as discussed below.

REPRODUCTION

Courtship and mating.—Despite extended field and laboratory observation, copulation or definite mating behavior of any sort was not observed.

Pre-depositional development of eggs.—The first eggs examined were those seen in dissections of freshly caught females. One specimen of April 7, 1947 contained three globular yellow eggs, 2.5 mm. in diameter. They were without shells. Another of the same date had two eggs in each oviduct, measuring 4 mm. in diameter. A large female of April 10, 1947 had four oval eggs, 7 mm., 8 mm., 9 mm., and 9 mm. in length. These eggs were without a definite shell. On July 14, two adult females were opened. One contained a globular ovum 3 mm. in diameter, while the second contained two fully developed oval, shelled eggs 9 mm. in length. These were filled with an amorphorus yellow yolk.

Deposition of eggs.—A number of lizards were maintained in the laboratory during March-August 1947. Six females produced eggs.

Female No. 1: On June 28, 1947, two young lizards and one egg 11 mm. in length were discovered in the cage. The egg contained a fully developed living infant. Deposition date was not recorded.

Female No. 2. A female captured July 1, 1947 produced three eggs in the first 48 hours. The eggs were found in a group under a grass clump, and measured 10 by 6 mm., 9.5 by 5.5 mm., and 10 by 5 mm. The shells were

leathery, dull white with a faint peach tint. The shells were tense, but easily dented with the fingernail. They hatched on the 33rd day (Aug. 7, 1947). The three young were bright copper in color, very active and agile. They were very soon eaten by the female. The shells were wrinkled, damp, and still buried in packed earth.

Female No. 3: A female taken July 5, 1947 produced three eggs on July 10. These were deeply buried in the humus of the cage. Their average weight was 145 gm., average size 9.5 by 4.5 mm. The eggs had a pinkish blush on the embryo side. These were observed during hatching on the 29th day and will be described below.

Female No. 4: A very fat female was taken Aug. 5, 1947. She produced one egg on Aug. 10, 1947 which hatched Sept. 11.

Female No. 5: This individual produced two eggs. The date of their deposition was not known. They failed to hatch.

Female No. 6: This large dark brown lizard captured July 15, 1947 did not bury her two eggs in a group, but scattered them over the humus of her cage. They were found July 20, 1947, one wrinkled, flabby, and brown, the other normal in appearance and measuring 11 by 7 mm. It was incubated but did not hatch.

Although the caged female *Leiolopisma* ordinarily prepares a rude nest for her eggs in humus, and groups her entire clutch in this nest, no evidence of further care or interest in the reproductive process was observed. In fact, the newly-hatched young may be eaten. Carr (1940) says the eggs are deposited in decaying wood, and that they are usually three in number.

Hatching.—The eggs of clutch #3 (laid July 10, 1947) were removed from the nest on August 8, 1947 and re-measured. They had increased in average size from 9.5 by 4.5 to 10 by 6.7 mm. The shell had become dirty, blotchy grey in color, leathery in consistency. During the process of weighing, the eggs lay on a wooden table top, under the warming rays of a desk light. They were observed to be moving about with irregular, erratic motions in first one direction, then another, due to violent motions of the contained embryo. The eggs soon began to hatch in succession, the details essentially as in the first to initiate the process.

5:17 P.M.—First motion of the egg.

5:19 P.M.—A slit 2 mm. in length appeared on side of egg, followed by an exuded drop of amber, serum-like fluid. This fluid appeared to soften the surrounding shell and make it more pliable. Four of these slits were made, at widely separate places on the sides and ends of the egg.

5:26 P.M.—After much violent thrashing by the embryo, the head was thrust suddenly through one of the previously formed slits, and moved about with lateral jerking motions. Respirations were about 70/min.

6:17 P.M.—After intermittent violent activity and rest, the eyes opened, and the lizard struggled to free its body.

6:35 P.M.—Left front leg emerged.

6:40 P.M.—Right front leg emerged.

6:43 P.M.—Hind legs emerged.

6:45 P.M.—Free of the egg. The lizard measured 42 mm. in total length. Dorsal color light brown, darker on the tail. Two distinct paradorsal lines of confluent dark spots, and lateral lines of darker brown were present. There was a rosy translucency of the post-axillary region.

The second egg required 2 hours 15 minutes to hatch, the third 2 hours 10 minutes. Hatching would possibly have been more rapid if the shells had not dried and hardened. When they were dampened, at the end of 2 hours, hatching progressed to completion within a few minutes. The lizards emerged from the shells through slits 5 mm. in length. When the slit was extended a globular yellow yolk remnant was seen, 3 mm. in diameter, and covered with a network of fine blood vessels. The young lizards were active and alert. They ran from a moving finger, and when placed in loose humus, promptly sought cover by thrusting their way through the loose material.

Appearance and behavior of wild juveniles.—Wild juveniles were first seen June 30, 1947. The first two were collected in very wet grass about 6 o'clock P.M. They weighed .143 and .144 gm., and measured 21 mm. snout-vent length, tail 29 mm. On July 1, 1947, three young were captured whose average weight was .146 gm. During July lizards continued to hatch, as evidenced by the variations in size of the captured specimens. A group of 15 juveniles taken July 29, 1947 and judged to be of recent hatching by comparison with a few definitely larger juveniles taken the same day, had an average individual weight of .138 gm. The young lizards were most numerous along abandoned lumber roads where they took refuge in cracks in the dried mud of the ruts.

Description of young.—An average wild juvenile of the weight and measurement range given above, presents an appearance much like the adult. The head, however, is larger in proportion, its dorsal color bright copper fading on the neck to a light brown. The dorsal band is of this color, patterned with irregular longitudinal rows of fine black specks. The lateral line is dark brown, and is sharply defined both above and below. It extends well out on the tail. The sides below the lateral band are light grey with a more or less well marked irregular or continuous row of black spots. The ventral surface is pale grey with a pinkish wash.

FOOD AND FEEDING HABITS

Food habits in the laboratory.—*Leiolopisma* ordinarily subsists on the small arthropod fauna of the forest floor. In the laboratory adult lizards occasionally grew emaciated, even in the presence of an abundance of food. Most individuals throve, however, and accepted a wide variety of substances. Foods

avidly sought were small diptera, roaches, moths, leaf hoppers, and finely ground beef or liver, either in stationary lumps or animated on the tip of a straw. Foods infrequently accepted were isopods (sow bugs were worried apart or crippled, but seldom actually consumed), maggots, buffalo bugs, meal worms, and pupae of flies. Snails and centipedes were never eaten.

Sufficient food supply for the laboratory lizards was always a problem. The contents of insect sweep nets passed through grassy meadows or brushland were supplemented by cultured drosophila and house flies. Quite surprising was the voluntary consumption of ground beef and liver, although live food was always preferred. Lizard activity normally ceased at dusk, but caged individuals learned to arouse themselves when lights were turned on at night in anticipation of a feeding. Many days they were fed between 8 P.M. and 12 P.M., or later. The presence of observers in the room, whether at mid-day or at mid-night would bring the older captives out seeking attention.

Food habits under natural conditions.—In addition to foods utilized under artificial conditions, habits and preferences in the field were studied. Three samples of about 20 fecal boluses were gathered from the inside of collecting boxes. The samples were macerated in water and preserved with formaldehyde. Mr. Pulley of the University of Houston describes the samples as follows:

Sample 32: Several masses of undigested insect remains consisting of pieces of exoskeleton felted together with insect hairs.

Sample 33: Many small bits of arthropod chitinous exoskeleton too fragmentary to identify, also a mass of what appears to be dirt and leaf mold.

Sample 34: Same as Sample 33.

Examination of the feces thus yielded little information. Analysis of stomach contents was more rewarding. Twenty-five adult lizards and twenty-five juveniles were killed and preserved as soon as captured. Mr. Pulley has very kindly identified as far as possible the fragmented material removed from the stomachs and intestines. His findings appear in table 1. The adults were taken in April, June, and July. The juveniles in late July 1947. No significant monthly differences in the contents of the adult stomachs were noted. Since volumetric estimation of stomach contents was judged highly inaccurate, only the relative frequency of food items is recorded. Amphipods may seem to be an unusual dietary item of a terrestrial lizard. These crustaceans are common in the shallow ditches and seep water of the area studied, and it may be imagined that *Leiolopisma* captures them as surface waters dry and disappear.

Digestion of food.—The rate of digestion was approximated by measuring the ingestion-defecation time. Twelve adult lizards were starved for ten days and then isolated in large watch glasses. Several dozen *Drosophila* were introduced into the containers at 9 A.M. July 27, 1947. Fecal material was first recorded at 2 P.M. July 28, 1947, and by 6 P.M. of that date all cages had one or more fecal masses, indicating a digestion rate of 29-33 hours.

TABLE 1.—Stomach contents of *Leiolopisma laterale* under natural conditions

Type of animal eaten	Number of stomachs in which found		Relative frequency of occurrence	
	Adult	Juvenile	Adult	Juvenile
Hymenoptera				
Formicidae	2	2	2	16
Vespidae	4	1	4	3
Diptera				
Adults	1	0	1	0
Pupae	1	0	1	0
Coleoptera				
Adults	3	2	4	5
Pupae and larvae	3	5	6	5
Homoptera	2	1	2	0
Collembola	1	0	1	0
Thysanoptera	0	1	0	1
Orthoptera				
Adults and nymphs of Ellipes minuta	1	4	3	9
Locustidae	1	0	1	0
Unidentified insect fragments, pupae, etc.	6	5	7	5
Chilopoda	2	0	2	0
Arachnida	2	5	2	5
Amphipoda	3	5	3	7
Gastropoda (terrestrial)	1	0	1	0
Nematode parasites	4	2	4	2
Annelida (earthworm)	1	0	1	0

Cannibalism.—Cannibalism was inevitable if small juveniles were kept in cages with adult lizards, even when other food was plentiful. One large female consumed five newly hatched young (not her own) within an afternoon. The remains were recovered from her stomach. Adults caged more than a few days showed missing toes and tail tips, autopsy revealing the missing members in the stomachs of other and usually larger cage-mates. Many lizards in communal cages met deaths of violence from fighting, with no apparent sex immunity. Autophagy was not observed.

Water consumption.—The laboratory lizards required water at least once daily. Droplets sprinkled on the glass cage walls or on vegetation were licked off avidly. Water was not taken from shallow dishes.

PARASITES AND ENEMIES

These small vertebrates probably have a number of enemies. The stomach of a copperhead killed in Houston July 15, 1947 contained four adults. Shrikes were occasionally seen consuming these skinks in the area studied. Except for Mr. Pulley's notes, the parasites of this lizard do not seem to have been studied.

ECONOMIC SIGNIFICANCE

Except for its insectivorous habits, *Leiolopisma* is probably of minor economic importance.

REFERENCES

BRIMLEY, C. S. 1939-1943—The amphibians and reptiles of North Carolina. Carolina Tips, 2-6: 64 pp., 22 figs.

BURT, C. E. 1928—The lizards of Kansas. Trans. St. Louis Acad. Sci., 26: 1-81.

———1935—Further records of the ecology and distribution of amphibians and reptiles in the Middle West. Amer. Midl. Nat., 16: 311-366.

CARR, A. F., JR. 1940—A contribution to the herpetology of Florida. Univ. Florida Publ. Biol. Ser., 3(1): i-iv+1-118.

CONANT, ROGER 1938—The reptiles of Ohio. Amer. Midl. Nat., 20: 1-200, 26 pls., 38 maps.

COOK, F. A. 1942—Alligator and lizards of Mississippi. Bull. Miss. State Game and Fish Comm., i-iv+1-20.

FORCE, E. R. 1930—The amphibians and reptiles of Tulsa County, Oklahoma, and vicinity. Copeia, (1): 25-39.

GLOYD, H. K. 1928—The amphibians and reptiles of Franklin County, Kansas. Trans. Kansas Acad. Sci., 31: 115-141.

MCCAULEY, R. H., JR. 1939—Notes on the food habits of certain Maryland lizards. Amer. Midl. Nat., 22: 150-153.

MOORE, J. P. 1896—Lygosoma (Liolepisma) Laterale in New Jersey. Amer. Nat., 30: 752-753.

RUTHVEN, A. G. AND L. C. STUART 1932—Notes on the period of post-depositional development in several common lizards. Occ. Papers Mus. Zool. Univ. Mich., No. 241: 1-3.

SLATER, J. A. 1949—Food habits of the brown skink, *Leiolopisma laterale* Say. Herpetologica, 5(3): 79-80.

SMITH, H. M. 1946—Handbook of lizards. Comstock Publ. Co. Inc., 557 pp., 136 figs., 41 maps. 134 pls.

STRECKER, J. K. 1910—Notes on the fauna of northwestern Texas. Baylor Univ. Bull., 13: 1-31, 2 figs.

Amphibians and Reptiles of a Fifteen-Acre Tract in Georgia

Wilfred T. Neill

Research Division Ross Allen's Reptile Institute, Silver Springs, Florida

In the Piedmont region of Georgia, about four miles northwest of Augusta, Richmond County, lies a fifteen-acre tract of creek bottomland that supports a varied population of small creatures. I have studied the herpetofauna of this tract intensely since 1932, collecting sparingly but compiling voluminous notes. In September, 1946, an instantaneous population census of the reptiles and amphibians was made and the findings compared with observations over a period of years.[1]

History.—On the hillsides bordering the tract are found the artifacts of an ancient Indian culture, but what effect the aborigines had on the ecology of the area can only be surmised. Early deeds indicate that the locality was part of a plantation in 1773. Intensive cultivation has reduced much of the surrounding land to barren red-clay fields. The general area was never thickly settled, however, and the creek valley itself was probably never under cultivation. In 1900 the bottomland supported a forest of large trees. About 1920 some of the larger trees were felled to promote the growth of grass. The area was then utilized as pasturage for a small herd of cows, and has been grazed over ever since. Each year since 1920 a few more large trees have been cut down, the fallen timber being left in place.

General description.—At present the pasture is open and park-like, the ground covered thickly with grasses but with few shrubs or forbs. Large trees are numerous, in places forming thick stands. Rotting stumps and logs litter the ground. Two small streams unite in the area to form a swift creek twelve to fifteen feet wide and one to four feet deep. Numerous temporary ponds and rivulets form during the winter and spring months. The bottomland, of course, provides a continuous habitat along the creek for several miles; yet above and below the pasture the aspect is very different, the trees being smaller and more thickly clustered, the underbrush dense. The valley is bordered by a patchwork of cultivated fields, old fields, stands of scrubby pine, and thickets of shrubs and vines.

Climate.—In the Augusta area the average winter temperature is 48.5 degrees F., with a variation of 39 to 58 degrees for different years; the average summer temperature is 80 degrees, varying from 71 to 90 degrees. The average date of the last killing frost in the spring is March 14, varying from

1 I am indebted to Messrs. I. G. Rucker, Jr., Joseph P. Bailey, Jr., Francis L. Rose, and Robert L. Humphries for assistance in studying the local herpetofauna.

February 2 to April 17; the average date of the first killing frost in the fall is November 13, varying from October 21 to December 26. Average rainfall is 44.9 inches per year, occurring on an average of 112 scattered dates.

Flora.—Within the pasture the predominant tree is the swamp chestnut oak (*Quercus prinus*), with large numbers of white oak (*Q. alba*), water oak (*Q. nigra*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), tulip tree (*Liriodendron tulipifera*), black gum (*Nyssa sylvatica*), American elm (*Ulmus americana*), hop hornbeam (*Ostrya virginiana*), blue beech (*Carpinus caroliniana*), pignut hickory (*Carya glabra*), red haw (*Crataegus* sp.), American holly (*Ilex opaca*), and river birch (*Betula nigra*).

Conspicuous elements of the flora are numerous vines, many of remarkable size, including rattan (*Berchemia scandens*), wild grape (*Vitis* sp.), possum grape (*Cissus* sp.), bamboo-vine (*Smilax laurifolia*), poison ivy (*Toxicodendron radicans*), and a climbing ericad (*Ampelothamnus phillyreifolius*).

Small bushes and shrubs are almost entirely lacking. Commonest forbs include thistles (*Cirsium* sp.), bitter-weed (*Helenium tenuifolium*), nigger-weed (*Pluchea foetida*), mullein (*Verbascum* sp.), poke-weed (*Phytolacca americana*), and black-berry (*Rubus* sp.).

Mammals.—The mammalian fauna is scanty. The surrounding woods and fields occasionally harbor the gray fox (*Urocyon cineroargenteus* subsp.), the red fox (*Vulpes fulva*), the possum (*Didelphys virginiana* subsp.), deer mice (*Peromyscus* spp.), rabbits (*Sylvilagus floridanus mallurus* and *S. a. aquaticus*), and shrews (*Blarina brevicauda carolinensis* and *Cryptotis p. parva*). All of these avoid the pasture, perhaps on account of its open aspect. Gray squirrels (*Sciurus c. carolinensis*), flying squirrels (*Glaucomys volans saturatus*), raccoons (*Procyon lotor* subsp.), muskrats (*Ondatra z. zibethica*), moles (*Scalopus aquaticus howelli*), and several kinds of bats are occasionally noted in the pasture. Fifteen to twenty cows graze over the area for several hours daily.

Birds.—The southeastern bird fauna is well represented. The larger species are the eastern red-tailed hawk (*Buteo jamaicensis borealis*) and the Florida red-shouldered hawk (*B. lineatus alleni*), which are often noted foraging over the open spaces or perching in the tops of lofty trees; vultures (*Cathartes aura septentrionalis* and *Coragyps atratus*); the southern crow (*Corvus brachyrhynchus paulus*); the southern screech owl (*Otus a. asio*); and the Florida barred owl (*Strix varia georgica*).

Fishes.—The commonest stream fishes includes three cyprinids (*Notropis lutipinnis, Semotilus atromaculatus* subsp., and *Nocomis* sp.), the red-finned pike (*Esox americanus*), the top-minnow (*Gambusia affinis holbrookii*), the eel (*Anguilla bostoniensis*), a darter (*Boleosoma nigrum* subsp.), and the bluegill (*Lepomis macrochirus*).

Invertebrates.—The temporary ponds swarm with invertebrates, from protozoa to annelid worms and amphipods. In the stream there are numerous crayfish and fresh-water shrimp. Beneath debris in the pasture there are numbers of earthworms, snails, slugs, centipedes, millipedes, scorpions, lycosid spiders, black widow spiders, crickets, carabid and lucanid beetles, and a host of other forms. Fallen timbers are riddled with tunnels of a passalid beetle (*Passalus cornutus*), by various cerambycid, scarabaeid, and elaterid beetles, and by termites.

Census.—On September 30, 1946, the writer, assisted by several zoology students from the Augusta Junior College, attempted to make a census of the amphibian and reptile population. The date was selected because weather conditions had been normal for some time previously. During the day each bit of cover was overturned and the underlying debris raked. Bark was stripped from rotting stumps and logs. Streams and ponds were investigated with seine and dip-net. Open ground, stream margins, tree trunks, etc. were carefully scanned. Much of the night was spent in going over the area with flashlights, particular attention being paid to the creek banks, which yielded many frogs that had been concealed during the day. Specimens found were confined for the period of the search; most were subsequently released. Results of the census were as follows (numbers refer to transformed examples except as otherwise noted):

Salamanders: Amphiuma means 1; *Triturus v. viridescens* eft 1; *Ambystoma opacum* 25; *Desmognathus fuscus auriculatus* 30; *Plethodon g. glutinosus* 2; *Pseudotriton montanus flavissimus* 3, larva 1; *Eurycea bislineata cirrigera* 9, larvae 9; *E. longicauda guttolineata* 2.

Frogs: Bufo t. terrestris 5; *Acris crepitans* 343; *A. g. gryllus* 2: *Pseudacris nigrita feriarum* 4; *Rana catesbeiana* 3, larvae 4; *R. clamitans* 12, larvae 12; *Rana pipiens sphenocephala* 27; *Microhyla c. carolinensis* 9.

Lizards: Anolis carolinensis 9; *Sceloporus undulatus hyacinthinus* 8; *Leiolopisma laterale* 12; *Eumeces fasciatus* 5; *E. inexpectatus* 10; *E. laticeps* 2.

Snakes: Diadophis p. punctatus 9; *Storeria dekayi wrightorum* 4.

Turtles: Kinosternon s. subrubrum 3; *Chelydra s. serpentina* 1; *Terrapene c. carolina* 16.

Thus the survey revealed the presence of 72 transformed and 11 larval salamanders, representing 8 species; 405 frogs and 16 tadpoles of 8 species; 46 lizards of 6 species; 13 snakes of 2 species; and 20 turtles of 3 species—a total of 583 individuals of 27 species.

Two other forms were certainly present in the pasture at the time of the survey: the subterranean *Ambystoma maculatum* and the arboreal *Hyla v. versicolor*. Other species that have been noted in the pasture from time to

time include *Hyla c. crucifer, Bufo woodhousii fowleri, Cnemidophorus sexlineatus,* and *Natrix e. erythrogaster.* Two *Pseudotriton ruber vioscai,* three *Natrix sipedon pleuralis,* and one each of *Storeria o. occipitomaculata, Thamnophis o. ordinatus, Chrysemys p. picta,* and *Pseudemys f. floridana* have been noted in the bottomland since 1932.

A number of forms have been noted in the vicinity, often up to the edge of the pasture but never within it. Some of these may be dismissed from consideration because of their general rarity in the region. Such are *Ambystoma talpoideum, Hemidactylium scutatum, Scaphiopus h. holbrookii, Hyla gratiosa, Farancia a. abacura, Pituophis m. melanoleucus, Haldea v. valeriae,* and *Crotalus horridus atricaudatus.* Species common in the general area but found in a drier habitat than the pasture are *Masticophis f. flagellum, Cemophora coccinea, Haldea striatula,* and *Tantilla c. coronata.* It is difficult to explain the absence of *Hyla c. cinerea, H. squirella, Ophisaurus v. ventralis, Heterodon p. platyrhinos, Opheodrys aestivus, Coluber c. constrictor, Elaphe guttata, E. o. obsoleta, Lampropeltis g. getulus, Natrix septemvittata, Thamnophis s. sirtalis,*[2] *Agkistrodon c. contortrix,* and *A. p. piscivorus,* all of which are common in the general area but apparently lacking in the bottomland tract.

---

[2] The eastern ribbon snake (cf. Klauber, Copeia 1948: 1).

Notes on a Collection of Reptiles and Amphibians from Princess Anne County, Virginia

John E. Werler and James McCallion

San Antonio Zoological Society, San Antonio, Texas

Intermittently during 1942, 1943 and 1944, we assembled a collection of reptiles and amphibians from Princess Anne County, Virginia, representing 58 species and subspecies. With few exceptions, the forms listed are represented by preserved specimens, most of which are now in the collection of the Carnegie Museum, and in only a few cases, i.e., *Crotalus horridus atricaudatus*, *Ophisaurus ventralis ventralis*, *Malaclemys centrata concentrica* and *Triturus viridescens viridescens*, are records based merely upon specimens observed in the field but not preserved.

In view of the fact that a number of workers are at present engaged in a study of the herpetofauna of the Dismal Swamp region (The Dismal Swamp region as outlined by Kearney (1901) includes a large portion of Princess Anne County), and since considerable time may lapse before a thorough study of the collection can be made, we consider it advisable to make available to these workers and others this preliminary list, pending a more detailed study at a later date.

We wish to acknowledge our thanks to the following persons for their help and for the many courtesies which they extended: Carl F. Kauffeld, Staten Island Zoological Society; Roger Conant, Philadelphia Zoological Society; M. Graham Netting, Carnegie Museum, Robert Mathewson, Staten Island Academy of Arts and Sciences and Stanley Zapolski of Detroit, Michigan.

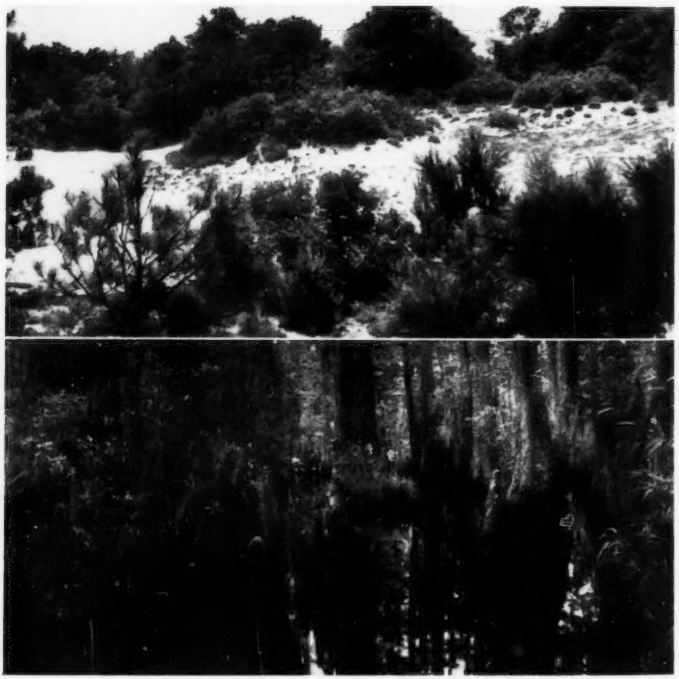
Princess Anne County is located on the Atlantic Coastal Plain at the extreme southeastern corner of Virginia; being bordered on the north by Chesapeake Bay, on the east by the Atlantic Ocean, on the south by Currituck County, North Carolina and on the west by Norfolk County, Virginia. With the possible exception of the Cape Henry Dune area, located at the extreme northeast corner of the County and having a maximum elevation of thirty meters, Princess Anne County is typical of the Dismal Swamp Terrace, as outlined by Wentworth (1930). A narrow fringe of Princess Anne Terrace margins the County on the extreme north and east.

Since most of our collecting was centered in and about the Seashore State Park, it is advisable to include a short description of this area, of which Egler (1942) writes, in part:

> The topography of Cape Henry may be said to be a succession of crescentic dune ridges, approximately paralleling the present shore line. They vary from a few meters above sea level to a height of 30 m. (the highest elevation of southeastern Virginia), and are separated by more or less extensive swamps lying approximately at sea level. . . . Swamp lands predominate in the interior of the Park with widely spaced low dune ridges. . . . Lying about half a mile from the present beach is the Great Dune, a single large

ridge with a clearly defined lee slope. . . . The inorganic parent material of all the soils of the State Park is siliceous beach sand of uniform texture and composition. . . . In low-lying areas, organic material accumulates, which varies from a thin muck layer overlying essentially unmodified sand, to muck deposits probably several meters in depth.

The proportionately varied topography peculiar to this Coastal Plain area, particularly within the Seashore State Park, and the resulting number of rather distinct habitat areas, prompted us to present the following annotated list of the County's reptiles and amphibians with their corresponding habitat areas instead of by the many localities as they appear in the field notes. Each area is, in most instances, characterized by the predominance of one type of plant association and this is often accompanied by a marked physiographic feature. With a few exceptions, key letters alone indicate the localities for each form.



Figs. 1, 2.—1. (upper) At the periphery of the Great Sand Dune of Area Aa. This habitat is occupied by *Bufo terrestris, Bufo woodhousii fowleri, Sceloporus undulatus hyacinthinus, Cnemidophorus sexlineatus* and *Cemophora coccinea;* 2. (lower) Cypress pool area Ac in the Seashore State Park at Cape Henry. Typical representatives of this area include *Triturus viridescens viridescens, Ambystoma opacum, Rana virgatipes, Caphophis amoena, Diadophis punctatus punctatus, Natrix erythrogaster erythrogaster* and *Chelydra serpentina.*

HABITAT AREAS

Aa *Seashore State Park, sand dune area.*—A single, large sand ridge, thirty meters high and devoid of vegetation except for beach and panic grass and scattered individual bayberry and pine trees. Considerable growth is found at the periphery of the Dune.

Ab *Seashore State Park, sand ridge area.*—A series of widely spaced dune ridges, much lower than in area Aa, being from six to ten meters high and supporting a rather dense growth of pine-oak-hickory association.

Ac *Seashore State Park, cypress pool area.*—The characteristic feature of this area is the almost complete dominance of the cypress in and around the low-lying pools, with black gum occurring frequently on the slightly higher sites. Spanish moss reaches its greatest profusion in the vicinity of these pools. This forest community, which occurs on all sites between dune ridges Ab, where the water is at or above soil surface, supports an accumulation of organic matter which may be as much as several meters deep.

B *Virginia Beach Township.*—Immediately to the south of the Seashore State Park and adjacent to the Atlantic Ocean, this area includes Crystal Lake, Lake Tecomseh and several smaller fresh water lakes and ponds which are, as a rule, margined with cat-tail marshes.

C *Four miles west of Virginia Beach.*—A heavily shaded glen of predominantly hardwood forest, traversed by a slow-running, fresh water stream. Peculiar to this area is an abundant growth of ferns and *Arisoema tryphyllum* plants.

D *Oceana and London Bridge Townships.*—This region of mixed pine and oak is extensively farmed and much of the land has been cleared for military installations.

E *West Neck Creek and Pungo Township.*—This area is traversed by fresh water West Neck Creek, a tributary of North Landing River, and extends approximately ten miles in a north-south direction through the center of the County. The Creek is margined principally with cypress and cedar and the adjacent higher sites support dense pine growths. Collecting along the Creek was centered at a point about two miles southwest of Pungo Township.

F *Princess Anne Township.*—This area of mostly hardwood forests is well watered by a dendritic pattern of small, fresh water streams.

G *Dam Neck Township.*—Extensive brackish marshes and occasional cedar swamps margin the beach side of this area while pine woods are found to the west.

H *Barrier beach area.*—The barrier beach, beginning approximately at Dam Neck and extending south off the southern third of the County, is separated from the mainland by brackish North Bay, Red Head Bay, Sandy Bay and Back Bay. Its western edge supports intermittent mixed deciduous and pine woods as well as scrub swamps and open marshes. In many places this narrow strip of land is not more than several hundred yards wide.

ANNOTATED LIST OF SPECIES

Amphiuma means means Garden, C.—This species was rarely seen, and then only at night. Specimens taken by us were observed using crayfish burrows in stream bottoms as retreats, and on two occasions the salamanders were lured from their holes by slowly waving a finger in front of the crayfish burrows to simulate living prey.

Triturus viridescens viridescens (Rafinesque), Ac.—Two efts of this form were taken during the summer of 1944 beneath moist logs in the vicinity of a cypress pool and no others were observed in the County.

Ambystoma opacum (Gravenhorst), Ac.—Specimens of this species were found in numbers only during the spring, when often two or three individuals were taken from under a single decaying log.

Desmognathus fuscus fuscus (Rafinesque), C, D.—These salamanders were collected

in numbers during several night collecting trips to area C, August 25 and 29, 1944. Here they were found only in and about a restricted portion of a small, sand-bottomed stream to which they would invariably retreat when disturbed. A single additional specimen was taken at London Bridge Township from beneath a large tree limb lying in moist, loamy soil.

Plethodon cinereus cinereus (Green), F.—Few specimens of this form were collected in the County, and then only from beneath or within moist, rotting logs in shaded woods.

Plethodon glutinosus glutinosus (Green), Ac, B, C, D, E.—Everywhere common, this most abundant of the salamanders was found wherever there was a sufficient moisture and suitable cover. As many as eight individuals were found under a single decaying log.

Stereochilus marginatus (Hallowell), B, C.—Only two specimens of this form were taken in the County. One of these was found under a partially submerged log in a clay pit between Virginia Beach and Oceana.

Figs, 3, 4.—3. (upper) Hardwood glen four miles west of Virginia Beach Township. The favored habitat of *Amphiuma means means, Desmognathus fuscus fuscus, Eurycea bislineata bislineata, Diadophis punctatus punctatus* and *Agkistrodon mokeson austrinus;* 4. (lower) West Neck Creek in area E. The most characteristic reptiles and amphibians of this predominantly cypress and cedar area are: *Plethodon glutinosus, Natrix taxispilota, Thamnophis sauritus sauritus, Agkistrodon piscivorus piscivorus* and *Chrysemys picta picta.*

Fig. 5.—The most heavily wooded portion of the barrier reef (area H) is its northern terminus, near Dam Neck Township. Here are found *Hyla cinerea cinerea, Gastrophryne carolinensis, Ophisaurus ventralis ventralis, Coluber constrictor constrictor, Storeria dekayi dekayi, Lampropeltis getulus getulus* and *Agkistrodon piscivorus piscivorus.*

Eurycea bislineata bislineata (Green), C.—Numerous larvae of this form were found in company with *Desmognathus fuscus fuscus* in the sand-bottomed stream of area C, and during the nights of August 29 and 30, 1944, 83 larvae were taken here. The adults confined themselves to the sloping sides of the adjoining hills.

Bufo terrestris (Bonnaterre), Aa, Ab, Ac, B, C, D.—The earliest and latest collecting dates for this common species are May 3 and August 29, respectively.

Bufo woodhousii fowleri (Hinkley), Aa, Ab, B.—Only fairly common and taken only in the northern part of the County.

Acris gryllus gryllus (Le Conte), Ac, B.—This frog was most abundant in the cypress pools of the Seashore State Park. A chorus was heard calling on March 4, 1942 at a small pond on Bird Neck Point, near the northern limits of Virginia Beach Township.

Pseudacris brimleyi Brandt and Walker, B.—A chorus of these frogs was heard calling on March 4, 1942 from a small *Typha* pool at Virginia Beach but no others were observed in the County. Two specimens are in the collection.

Hyla cinerea cinerea (Schneider), Ab, B, H.—Frogs of this subspecies were calling in chorus on the night of June 30, 1944 along the shore of a large pond at Virginia Beach. They were commonly found along the marshy sections of the barrier reef atop twenty foot telephone poles, between the poles and crossarms. Parallel aerial habits of this species were observed along the marshy coast of southeastern Texas where, again, these frogs utilized the space between the telephone poles and crossarms as retreats. Of ten preserved specimens, six possess a white lateral stripe which extends backward to the groin; in three the stripes extend almost to the groin, and one young specimen is without any trace of a stripe.

Hyla crucifer crucifer Wied, Ac, D.—Only two specimens of this frog were collected. One was taken March 7, 1943 near Thomas Corners and the other was found in the Seashore State Park on a cypress knee where it perfectly simulated the lichen growth upon which it rested.

Hyla versicolor versicolor (Le Conte), Ac, E.—Rarely seen in the County. Although a stream was nearby, a specimen chose to utilize as a retreat a water-filled depression in a tree trunk four feet above the ground.

Rana catesbeiana Shaw, Ac, B, C.—Several individuals were calling from a pond at Virginia Beach, June 30, 1942. This species was common in the Virginia Beach area but less so elsewhere in the County.

Rana clamitans Latreille, Ac, B, D.—Fairly common. Tadpoles of this species were observed during the summer in cypress pools at Virginia Beach. In company with *Rana catesbeiana*, it was heard calling from a pond at Virginia Beach, June 30, 1942.

Rana pipiens Schreber, Ac, B, C, F.—Frequently observed in the northern part of the County and particularly abundant in certain pools at the Seashore State Park.

Rana virgatipes Cope, Ac.—The only specimen found by us was taken as it perched upon a cypress stump in a large cypress pool at the Seashore State Park, August 24, 1944.

Gastrophryne carolinensis (Holbrook), B, H.—Two specimens were found under boards at the edge of a brackish marsh which borders the western shore of the barrier reef. Two others were taken during the heat of a summer day from under logs, and a third from beneath a piece of cardboard in a sand lot at Virginia Beach. One of these was covered with a spittle-like substance which appeared to have been, in some way, secreted or otherwise formed by the frogs themselves.

Sceloporus undulatus hyacinthinus (Green), Aa, Ab, B, G.—Very common in the northern part of the County, especially within the Seashore State Park.

Ophisaurus ventralis ventralis (Linnaeus), H.—This subspecies is not represented in our collection by preserved specimens. One of these lizards was found dead in a shallow pool along the western edge of the barrier reef and several others were observed in the same area. Further south, where the reef extends out along the North Carolina coast, this lizard was much more common.

Cnemidophorus sexlineatus (Linnaeus), Aa, Ab, B.—Although abundant in the northeastern part of the County, this lizard was not observed south of Virginia Beach Township. Fairly common where found.

Leiolopisma laterale (Say), Ab, Ac, B.—This form was found in numbers throughout the year among dead leaves on the ground. Individuals were active as early as February and as late as December.

Eumeces fasciatus (Linnaeus), Ab, Ac, B, D, E, F.—The field notes for this species may apply also to *inexpectatus* and *laticeps* since none of the three forms was specifically identified in the field. This was the most common lizard of the Seashore State Park, where it was found most frequently beneath the loose bark of standing and fallen pine trees as well as in and under dry, rotting logs. On two occasions specimens were observed to eat tenebrionid beetles and larvae.

Eumeces inexpectatus Taylor, Ab, Ac, B, D, E, F.—See *Eumeces fasciatus*.

Eumeces laticeps (Schneider), Ab, Ac, B, D, E, F.—See *Eumeces fasciatus*.

Carphophis amoena amoena (Say), Ac.—The favored habitat of this species was wet decaying logs along the edge of cypress pools. Consistent collecting in this area yielded only four specimens, all taken during early spring. It must be considered rare in the County.

Farancia abacura abacura (Holbrook), Ab, Ac.—Two D.O.R. snakes of this subspecies were found in the Seashore State Park.

Diadophis punctatus punctatus (Linnaeus), Ac, C.—In the cypress pool area of the Seashore State Park, these snakes were taken from within wet, decaying logs in company with *Carphophis amoena amoena*. Three were secured from beneath wet, decaying logs in the hardwood forest of area C. None was found in the southern part of the County.

Heterodon contortrix contortrix (Linnaeus), B.—Only a single specimen of this snake was secured in spite of an abundant favorable habitat over much of the County, and reports by local inhabitants that it was common about the sand dunes of the Seashore State Park.

Opheodrys aestivus (Linnaeus), Ab, B, D.—This snake was taken during every month of the year except January, February and December, and can be considered one of the most common snakes in the County.

Coluber constrictor constrictor (Linnaeus), Ac, B, H.—Fairly common in the northern part of the County and along the entire length of the barrier reef; less so along the mainland in the southern part of the County. Although none was caught south of Virginia

Beach, we have reliable reports of its occurrence there. A female taken at Virginia Beach on June 24, 1942, laid four eggs on June 27, and one egg on each of the following days: June 28, July 1, July 3 and July 5. None of these eggs hatched.

Elaphe obsoleta obsoleta (Say), B, E.—Only three specimens were collected within the County and all were found crawling on the ground.

Lampropeltis getulus getulus (Linnaeus), B, E, H.—This king snake is decidedly partial to wet situations. Most were found beneath boards and logs in or near swamps or streams.

Lampropeltis triangulum temporalis (Cope) X *elapsoides* (Holbrook), Ab.—Three specimens, representing intergrades between the two forms *temporalis* and *elapsoides*, are numbers MCZ 46,730; 46,731 and 46,732 in the collection of the Museum of Comparative Zoology and have been reported upon by Conant (1943: plate 4, figs. 6 and 7). All were found during April and May of 1942 in well shaded woods of area Ab. Two were dug from within a large decayed pine log; a third was found under the loose bark of a standing pine stump, and another (not in the preserved collection) was coiled beneath a fallen tree limb. On numerous occasions these snakes fed upon *Eumeces* which were offered them, and in no case was constriction employed to subdue the lizards before ingestion. The prey was swallowed while still alive. That this snake is canabalistic was demonstrated on two different occasions when one individual seized and attempted to swallow its cage mate.

Cemophora coccinea (Blumenbach), Aa.—Rare in the County. Taken only from area Aa, under dry, rotted telephone poles along the lee slope of the dry and barren Great Dune. Represented in the collection by only two specimens.

Natrix erythrogaster erythrogaster (Forster), Ac.—Confined to regions of cypress growth in the Seashore State Park, this appeared to be the most terrestrial of the County's water snakes. Specimens were almost invariably found on land, and when pursued, entered the water to escape capture but returned to dry land almost immediately. This snake was fairly common in its restricted habitat.

Natrix sipedon sipedon (Linnaeus), Ac, G.—This snake was found in both fresh and brackish water. Since most specimens from the Seashore State Park lack lateral blotches and possess dorsal blotches which extend to the ventrals for the entire length of the body, they appear to intergrade at this point with *fasciata*.

Natrix taxispilota (Holbrook), E, F.—This species is confined to the cypress waters of the County, although never observed in the cypress pools of the Seashore State Park. In the spring, as many as three dozen specimens were collected in one day by rowing a boat along West Neck Creek where the snakes were draped about the bases of cypress knees along the edge of the water. An unusually large specimen, 1745 mm. long, was collected just south of Pungo Township.

Storeria dekayi dekayi (Holbrook), E, H.—Only two specimens of this snake were found in the County, both collected in the immediate vicinity of water.

Storeria occipitomaculata occipitomaculata (Storer), D.—The single specimen represented in our collection was found under the bark of a large tree limb, several feet above the ground, March 25, 1942.

Haldea valeriae valeriae (Baird and Girard), Ab, E.—Only two specimens were collected, both at the edge of cultivated fields.

Thamnophis sauritus sauritus (Linnaeus), E, G, H.—One of the most common snakes in the County. Seen in greatest numbers in the marshes along the coastal barrier reef.

Thamnophis sirtalis sirtalis (Linnaeus), F.—A single specimen was taken, crossing a paved road near Princess Anne Township, October 2, 1943. Abandoned fields bordered the road for perhaps a half mile on either side.

Agkistrodon contortrix contortrix Gloyd and Conant, C, E, F.—Uncommon in the County. Found only in dense deciduous woods in the northern half of the County.

Agkistrodon piscivorus piscivorus (Lacépède), Ac, E, F, H.—Several large adults

(one nearly five feet in length) are marked with unusually vivid crossbands and have an abnormally light ground color. This species was very common in areas E and H.

Crotalus horridus atricaudatus (Latreille), E.—Reports of this rattlesnake from the County are not uncommon. A D.O.R. specimen, nearly six feet in length, was found at Pungo Township, July 23, 1942, but not preserved. This snake had twenty-five scale rows at mid-body and the characteristic light-orange mid-dorsal stripe of this subspecies.

Sternotherus odoratus (Latreille), G.—This turtle was found only at Princess Anne Township in small fresh water streams.

Kinosternon subrubrum subrubrum (Lacépède), Ac, G.—Found in large numbers, especially at the Seashore State Park.

Chelydra serpentina serpentina (Linnaeus), Ac.—Common in the Seashore State Park area.

Clemmys guttata (Schneider), B, H.—Very common in the northern half of the County.

Terrapene carolina carolina (Linnaeus), B, D, G.—Very common. That turtles of this area frequently resort to aestivation during periods of prolonged drought is indicated by the following observations: On several occasions during the extremely dry spell of August, 1944, box turtles were found in aestivation, completely concealed in the ground with only their heads visible at the surface to indicate their presence. During a dry spell in June, 1942, and again in August, 1944, following a drought, turtles of several species were seen to aestivate in damp stream beds in various parts of the County. On June 25, 1942 several specimens of *Kinosternon*, one *Pseudemys* and a *Chelydra* in apparent aestivation were found dug in along the nearly dry bed of a drainage ditch in the Seashore State Park. Some thirty dead *Kinosternon*, in various stages of decay, lay scattered in or near the ditch, apparently unable to reach the moist section of the bed before the sun killed them.

Malaclemys centrata concentrica (Shaw), H.—Several specimens of this turtle were seen in the tide pools along the lower half of the barrier reef. Immediately to the south, in North Carolina, it is much more common.

Chrysemys picta picta (Schneider), B, E.—Moderately common in scattered localities.

Pseudemys floridana floridana (Le Conte), H.—The only specimen from the County was found on the mainland side of the barrier reef.

Pseudemys floridana concinna (Le Conte), B, H.—Abundant in the small pools at Virginia Beach.

Pseudemys rubiventris rubiventris (Le Conte), Ac B.—Very common in the cypress pools of the Seashore State Park.

REFERENCES

CONANT, ROGER 1943—The Milk Snakes of the Atlantic Coastal Plain. Proc. New England Zool. Club, vol. 22, pp. 3-24, pls. 2-5.

EGLER, FRANK E. 1942—Check List of the Ferns and Flowering Plants of the Seashore State Park, Cape Henry, Virginia. Mimeographed Publication, New York State College of Forestry, Syracuse, N. Y., pp. i-ii, 1-60.

KEARNEY, T. H. 1901—Report on a Botanical Survey of the Dismal Swamp Region. U. S. Nat. Herbarium Contr., 5 (6), pp. 321-585.

WENTWORTH, CHESTER K. 1930—Sand and Gravel Resources of the Coastal Plain of Virginia. Virginia Geological Survey, Bull. 32, pp. i-xiv, 1-146, pls. 1-19, figs. 1-154.

Hymenolepis hopkinsi, n. sp., a Cestode from the Black Duck*

Everett L. Schiller**

Department of Veterinary Science, University of Wisconsin, Madison

The knowledge of the cestodes parasitic in Anseriformes is very incomplete. This is especially true of forms inhabiting the ceca. These worms are generally small and very fragile forms which readily lose their scolices or rostellar hooks, or undergo other degeneration within a short time after the death of the host. For this reason they are not usually in a suitable condition for critical study. Emphasis should be placed upon the acquisition of fresh material for more thorough and comprehensive determination of such cestodes.

Examinations were made of 14 black ducks, *Anas rubripes*, collected from Horicon Marsh, Wisconsin. Eight of these birds were obtained alive, by trapping, and were killed immediately prior to autopsy. *Hymenolepis fausti* (Tseng Shen, 1932) was found to occur frequently in the ceca of these birds; however, on two occasions several specimens of another small cestode were encountered exclusive of others in this habitat. The literature discloses no knowledge of the existence of this form and, therefore, it is described herein as new.

Hymenolepis hopkinsi n. sp.

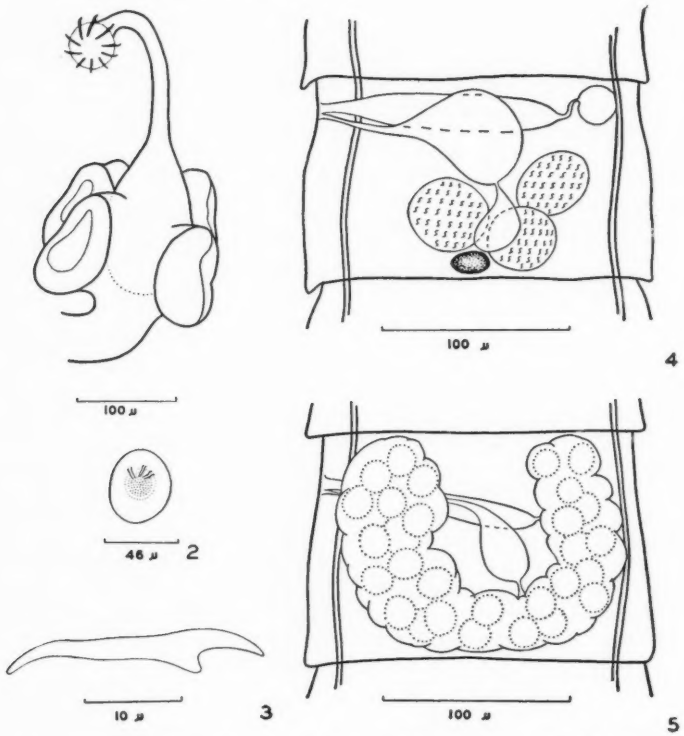
(Figs. 1-5)

Diagnosis.—Length of strobila 12 mm; maximum width 185 μ, attained at the posterior end. Scolex 142 x 170 μ. Evaginated rostellum 241 μ long, slender, measuring only 20 μ in diameter, enlarged to form a knob at the apex; latter is 29 μ in diameter and supports a single row of 10 hooks, 26 μ in length. Suckers unarmed, circular and heavily muscled; 102 μ in diameter. Strobila has a width of 33μ immediately posterior to base of the scolex. Segmentation begins 215 μ from scolex and the genital *Anlagen* appear in approximately the 70th proglottid posterior to point of beginning segmentation. Genital pores unilateral and sinistral, occurring in anterior 1/4 of the margin of the proglottid. Genital ducts lie dorsal to ventral excretory canals. Cirrus sac muscular, averaging 138 μ in length by 16 μ in diameter in mature proglottids. Cirrus sac extends transversely across proglottid to aporal ventral excretory canal. Internal and external seminal vesicles well developed. Exter-

* Supported in part by the Research Committee of the Graduate School from funds supplied by the Wisconsin Alumni Research Foundation. Project Leader: Dr. Banner Bill Morgan, Department of Veterinary Science, University of Wisconsin, Madison.

** Now with the U. S. Public Health Service, Box 960, Anchorage, Alaska.

nal seminal vesicle spherical, 33 μ in diameter in mature proglottids. External seminal vesicle lies directly aporal and slightly anterior to the terminal end of cirrus sac. Cirrus unarmed and without stylet. Sacculus accessorius lacking. Testes, three in number, subspherical, of equal size and arranged in form of a triangle. All testes lie in same plane, 36 μ in diameter and are enclosed by the ventral excretory canals. Ovary and vitelline gland are located in middle of proglottid. Saccate seminal receptacle lies ventral to cirrus sac and anterior to poral testis. Seminal receptacle very prominent in mature proglottids, where it attains a maximum diameter of 66 μ. Vagina ventral and posterior to cirrus sac. Uterus begins as a U-shaped structure, partially surrounding seminal receptacle and ovary, and enlarges to fill entire proglottid. Eggs range from 40 to 49 μ in diameter, few in number, 20 to 30 for each proglottid. Hook of embryo 10 μ in length.



Figs. 1-5.—*Hymenolepis hopkinsi* n. sp.—1. Scolex; 2. Egg; 3. Rostellar hook; 4. Mature proglottid (ventral view); 5. Post-mature proglottid with developing U-shaped uterus (ventral view).

Discussion.—Insofar as the writer is aware, *Hymenolepis jägerskiöldi* Fuhrmann, 1913, parasitic in Anseriformes, is the only other species known to possess a U-shaped uterus. It also resembles *H. hopkinsi* in containing only a small number of eggs (30 to 40). It differs, however, from the new species, somewhat in length, being smaller (2.5 mm to 5 mm, rarely 10 mm); the scolex is larger (180-210 μ in diameter), and the rostellum bears hooks of much greater length (42-45 μ) as well as being of a different shape. The external seminal vesicle is larger (68 μ) and the uterus does not extend beyond the excretory vessels.

Excepting the U-shaped uterus, 3 other small forms have been described which somewhat resemble *H. hopkinsi* in length of strobila (under 25 mm), size of rostellar hooks (between 25-30 μ) and are also lacking a cirrus stylet as well as a sacculus accessorius. For this reason a comparison with these 3 species seemed worthy of consideration. Notable differences are found to exist which further serve to distinguish these from the new species. The differences are enumerated as follows:

Hymenolepis fausti (Tseng Shen, 1932) (parasitic in Anseriformes) has a much smaller rostellum (20 μ), a larger cirrus sac (285 μ x 68 μ), a two-lobed ovary, and a sacciforme uterus. The rostellar hooks (28.8 μ in length) are of a distinctly different shape.

Hymenolepis magniovata Fuhrmann, 1918 (parasitic in Passeriformes) has smaller suckers (70 μ in diameter) and a shorter and broader rostellum (80 μ x 50 μ). The testes are arranged in a triangle but are smaller and widely separated. The rostellar hooks (30 μ in length) have a very different shape.

Hymenolepis spinosa von Linstow, 1906 (parasitic in Charadriiformes) has a larger scolex (220 μ), a spinose cirrus (28 μ in length) and differently shaped rostellar hooks.

A U-shaped uterus rarely occurs in this genus. This feature in combination with an unusually long slender rostellum relative to the size of the scolex, and the distinctive size and shape of the rostellar hooks are salient characters which readily differentiate this species from all others of the genus *Hymenolepis*. In view of the foregoing conclusions it seems justifiable to designate this species as new.

This species was named in honor of Mr. Ralph C. Hopkins, Game Biologist at Horicon Marsh, Wisconsin, who so generously provided live ducks from trapping operations carried on in connection with his waterfowl migration studies, thereby making the present study possible.

Thanks are also due to Dr. Banner Bill Morgan, Department of Veterinary Science, University of Wisconsin, for helpful suggestions during the course of this study.

Host.—*Anas rubripes* (black duck).

Locality.—Horicon Marsh, Wisconsin.

Habitat.—Ceca.

Type.—A slide, No. 46476, containing cotype material has been deposited in the Helminthological Collection of the U. S. National Museum.

REFERENCES

FUHRMANN, O. 1913—Nordische Vogelcestoden aus dem Museum von Göteborg Meddelanden fran Götebergs Musei Zologiska Afdelning 1, 41 p.

———1918—Cestodes d'oiseaux de la Nouvelle-Calédonie et des Iles Loyalty. F. Sarasin et J. Roux. Nova Caledonia, Zoologie, 2 (14): 399-449.

———1932—Les ténias des oiseaux. Mém. Univ. Neuchâtel., 8: 1-381.

HUGHES, R. C. 1940—The genus Hymenolepis Weinland 1858. Tech. Bull. Okla. Agr. and Mech. Coll. Agr. Exp. Sta., 8: 1-42.

———1941—A key to the species of tapeworms in Hymenolepis. Tr. Am. Micr. Soc., 40: 378-414.

JOYEUX, C. AND J. G. BAER 1936—Cestodes. Faune de France, 30: 1-613.

VON LINSTOW, O. 1906—Helminthes from the collection of the Colombo Museum. Spolia Zeylanica, 3 (2): 163-186.

TSENG SHEN 1932—Étude sur les Cestodes d'oiseaux de Chine. Ann. Paras. hum. comp., 10: 105-128.

(1)

n the

edde-

Sara-

Agr.

Soc.,

eum.

ıum.